

THE EFFECTS OF AREA AND SURFACE COMPLEXITY  
ON THE  
STRUCTURE AND FORMATION OF STREAM BENTHIC COMMUNITIES

by

William J. Trush, Jr.

Thesis submitted to the Graduate Faculty of the  
Virginia Polytechnic Institute and State University  
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

in

Zoology

APPROVED:

---

A. L. Buikema, Jr., Chairman

---

E. F. Benfield

---

J. Cairns, Jr.

January, 1979

Blacksburg, Virginia

## ACKNOWLEDGMENTS

I would like to thank my major advisor, Dr. A. L. Buikema, Jr., for his assistance throughout my studies. I also owe thanks to the other members of my committee, Dr. Ernest F. Benfield and Dr. John Cairns, Jr. I am grateful to

and other fellow graduate students for their encouragement. I owe very special thanks to Dr. Robert Butler from Penn State for his concern and, importantly, his time. The postman of Newport, , deserves a smile and thanks for his stream-side chats that made the cold winter water - not so cold.

## TABLE OF CONTENTS

	Page
ACKNOWLEDGEMENTS. . . . .	ii
LIST OF TABLES. . . . .	v
LIST OF FIGURES . . . . .	vii
GENERAL INTRODUCTION. . . . .	1
Stream Rocks as Islands . . . . .	1
PART I	
Species-Area-Surface Complexity Relationships . . . . .	4
INTRODUCTION. . . . .	4
METHODS . . . . .	5
RESULTS AND DISCUSSION. . . . .	13
Taxa-Area Relationship. . . . .	13
Surface Complexity Effects on the Taxa-Area Relationship. . . . .	29
An Empirical Model for Predicting Taxa Number . . . . .	34
Three Potential Surface Complexity Effects on Community Structure . . . . .	34
Effect of Area and Surface Complexity on Selected Taxa. . . . .	40
SUMMARY . . . . .	45
PART II	
A Functional Analysis of Stream Invertebrate Colonization. . . . .	47
INTRODUCTION. . . . .	47
Immigration . . . . .	48
Extinction. . . . .	49
Dynamic Equilibrium . . . . .	51
METHODS . . . . .	54
RESULTS AND DISCUSSION. . . . .	61
Colonization. . . . .	61
COL-substrate Community Structure . . . . .	69
Immigration . . . . .	79

	Page
Extinction. . . . .	91
Invasion and Replacement. . . . .	93
Comparison of COL-substrate Communities to the Immigration Pool . . . . .	98
SUMMARY . . . . .	105
PART III	
A Simulation of Benthic Community Colonization on Stream Substrates . . . . .	107
INTRODUCTION. . . . .	107
METHODS . . . . .	109
RESULTS AND DISCUSSION. . . . .	113
SUMMARY : . . . . .	119
PART IV	
Plans for the Coexistence of Taxa in Stream Invertebrate Communities . . . . .	120
GENERAL DISCUSSION. . . . .	120
Plan I. . . . .	120
Plan II . . . . .	126
Plan III. . . . .	130
Evaluation of Plans . . . . .	131
CONCLUSIONS . . . . .	135
LITERATURE CITED. . . . .	137
APPENDIX. . . . .	143
VITA. . . . .	150
ABSTRACT	

## LIST OF TABLES

Table	Page
1. Power and exponential functions: taxa-area regression models . . . . .	14
2. Power function: population size-rock area regression model . . . . .	20
3. Power function: population size-taxa number regression model . . . . .	21
4. Average densities (number of individuals / cm <sup>2</sup> ) for all taxa found on SIMPLE and COMPLEX rocks. . . . .	36
5. Population size - area regression models for taxa found on 10 or more rock macroinvertebrate communities. . . . .	41
6. Pertinent statistics in describing the colonization curves produced by periodic sampling of COL-substrates . . . . .	64
7. Average growth rates per sampling interval for each COL-substrate type. . . . .	68
8. Taxa list for colonization and immigration segments of Part II. . . . .	75
9. Average invasion and replacement rates for each sampling interval for all IMM-substrates. . . . .	94
10. Relative abundances within 7 major groups of taxa for all sampling intervals found on COL-substrate communities and IMM-substrate immigration pools. . . . .	99
11. Immigration, extinction, colonization, and growth rates in each sampling interval for simulated MEDIUM-COMPLEX COL-substrate communities . . . . .	115
12. Relative abundances of major taxa groups in simulated communities for Day 30. . . . .	117
A1. Stepwise regression results for Log S as the dependent variable and Log A, complexity and Log J as the independent variables . . . . .	144
A2. Coefficient of Similarity Index values among benthic communities found on rocks of similar size and complexity . . . . .	145

Table	Page
A3. Log transformed colonization curves for each COL-substrate community type. . . . .	146
A4. Comparison of taxa numbers between naturally occurring communities and Day 30 COL-substrate communities with the same area . . . . .	147
A5. Average daily immigration rates calculated over each time interval. . . . .	148
A6. Average daily extinction rates calculated over each time interval. . . . .	149

## LIST OF FIGURES

Figure	Page
1. Relationship between taxa diversity and Log area for SIMPLE, MODERATE, and COMPLEX rock communities collected in Sinking Creek. . . . .	16
2. Relationship between Log taxa diversity and Log area for SIMPLE, MODERATE, and COMPLEX rock communities collected in Sinking Creek. . . . .	18
3. Dominance - diversity relationships for communities on SMALL-SIMPLE and SMALL-COMPLEX rocks . . . . .	24
4. Dominance - diversity relationships for communities on LARGE-SIMPLE rocks . . . . .	26
5. Dominance - diversity relationships for communities on LARGE-COMPLEX rocks. . . . .	28
6. Colonization curves for each COL-substrate community type. . . . .	63
7. Dominance - diversity relationships for communities on SMALL-SIMPLE COL-substrates on Day 30 . . . . .	71
8. Dominance - diversity relationships for communities on MEDIUM-SIMPLE COL-substrates on Day 30 . . . . .	73
9. Cumulative immigration curves for COMPLEX IMM-substrates. . . . .	81
10. Cumulative immigration curves for SIMPLE IMM-substrates . . . . .	83
11. Day 30 cumulative immigration plotted as a function of IMM-substrate area . . . . .	85
12. Average SIMPLE IMM-substrate immigration rates for each sampling period. . . . .	88
13. Day 30 cumulative invasion plotted as a function of IMM-substrate area. . . . .	96
14. Cumulative colonization curves for simulated MEDIUM-COMPLEX substrate communities with 5, 10, and 20% extinction intensities . . . . .	114

## GENERAL INTRODUCTION

### Stream Rocks as Islands

Naturalists have long recognized a relationship between island area and the number of species inhabiting islands. It was not until Preston (1962) and MacArthur and Wilson (1963) independently proposed that island species numbers represented a dynamic balance between immigration and extinction. Though MacArthur and Wilson (1967) originally considered oceanic islands, their model has been expanded to describe any isolated, discrete patch of area surrounded by unlike terrain (see Simberloff, 1974, for a more complete definition). With this interpretation, flower blossoms (Seifert, 1975), cushion plants (Tepedino and Stanton, 1976), thistle heads (Brown and Kodric-Brown, 1977), and ponds (Lassen, 1975) are islands. Stream rocks have been considered islands for macrobenthic invertebrates and diatoms (Dickson and Cairns, 1972; Patrick, 1975; Stout and Vandermeer, 1975; Townsend and Hildrew, 1976). Stream rocks are insular in that the moving water column presents a barrier to immigration.

Immigration rates are considered to be dependent upon distance from the mainland; fewer species reach an island the farther it is from the mainland. Extinction rates are considered to be a function of island area, with smaller islands supporting fewer species. While it is intuitively appealing that greater distances from the immigration pool would result in lower immigration rates, a biological interpretation for why species extinction rates should decrease with increasing island area has not been resolved. For the last decade and more, it was

thought that the effect of area on extinction was dependent upon its high correlation with habitat complexity (MacArthur and Wilson, 1967). Greater habitat complexity would lower extinction rates by decreasing interspecific competition, permitting more species to coexist (see Smith, 1972, for further comment).

The actual proof of an increase in habitat complexity with increasing area has been more implicit than explicit. Due to the multidimensional nature of habitats, the qualification and quantification of "WHAT" and "HOW MANY" microhabitats are present on a given island is extremely difficult to assess. MacArthur et. al. (1962) found, for bird communities, that the selection and quantification of a physical variable (foliage height diversity) could serve as an indirect "measure" of habitat complexity. There have been few attempts at including physical variables as measurements of habitat complexity in species-area models (MacArthur and Wilson, 1967).

A physical variable which can indirectly measure habitat complexity for macrobenthic invertebrate communities is surface topography because many stream invertebrates on a rock are substrate specific (Percival and Whitehead, 1929; Scott, 1958; Hynes, 1970; Allan, 1975). A complex rock surface, having many surface variations (e.g. smooth patches, crevices, pores), can produce a wider range in other environmental variables such as a spectrum of water velocities (slow currents in eddies behind crevices; fast currents over smooth areas) or patterns of light and shade. Complex rocks, therefore, could offer immigrating species a greater number of potential microhabitats than simpler rocks (having predominantly smooth surfaces with few structural variations). The qualification

and quantification of rock surface complexity could serve as an indirect measure of habitat complexity for stream macrobenthic communities.

Throughout this paper stream rocks will be interpreted as islands. The objective of Part I is to document a possible species-area relationship for macrobenthic invertebrate communities on stream rocks and to assess the effect of surface complexity on community structure. In Part II, the functional aspects of macrobenthic communities are explored. Rates of immigration, invasion, colonization, and extinction are quantified for communities on different sizes and complexities of stream substrates. In Part III, substrate colonization is simulated through random processes of immigration and extinction and compared to actual macrobenthic colonization. Finally, in Part IV, several models for the coexistence of macroinvertebrates on rocks are presented and assessed through the literature and the results in the first three parts of this study.

## PART I

### Species-Area-Surface Complexity Relationships

#### INTRODUCTION

A principle characteristic of islands and a prediction derived from MacArthur and Wilson's equilibrium model (1963) is that species number increases on islands of progressively larger area. Preston (1962) predicted that the slope of this relationship, when plotted as a power function, should approximate 0.17 or 0.27, depending upon the degree of isolation for the islands under consideration. The species-area relationship and its similarity to Preston's prediction will be the primary topic of Part I. Because rocks differ in surface complexity, communities found on rocks of similar area but different surface complexities may differ in their number of species. The hypothesis, rocks with a complex surface support more diverse communities, will be tested by recording changes in the species-area regression slope and elevation for macro-invertebrate communities on rocks of varying surface complexities. The effect of area and surface complexity on other aspects of stream macro-invertebrate community structure will also be determined, utilizing measures of compositional similarity and relative abundance distributions.

PART I  
METHODS

The study site was located 300 m upstream from the State Route #42 bridge east of Newport, Virginia on Sinking Creek. Sinking Creek, a third order stream, flows through a valley under considerable agricultural pressure. At a site sampled by Hobbs (1975), just upstream from my sampling site, the mean yearly pH was 8.1 (a range of 6.9 to 8.8 over the year) and the maximum temperature was 24 C (a minimum of 0 C in January and February). Additionally, mean total hardness, total phosphate, and nitrate were 108 mg/l (yearly range of 75 to 135 mg/l), 0.201 mg/l (a yearly range of 0.070 to 0.322 mg/l), and 2.20 mg/l (yearly range of 0.90 to 3.40 mg/l), respectively (Hobbs, 1975). Oxygen concentration was at saturation throughout the year (Hobbs, 1975).

To determine a species-rock area curve, 48 rocks were selected from a section of stream riffle, 3 m by 4 m (collection was made on September 18, 1976). Average depth and velocity of the riffle sample area was  $17.5 \pm 2.1$  cm (SD) and  $12.0 \pm 2.3$  cm/sec (SD), respectively (55 measurements of depth and velocity). Several constraints governed the selection of each rock. Each rock had to be totally immersed, have no visible debris around its perimeter, have no contact with other rocks (other than the gravel matrix), and be directly exposed to the current. Rocks meeting the criteria were selected at random, carefully lifted from the bottom (at a slight downstream angle to reduce turbulence), and placed in individual containers. Downstream nets were not employed in transferring rocks from the streambed to the containers in order to avoid collecting organisms residing in the gravel matrix or on detritus trapped

beneath the rock. Although losses were undeniable, each rock was sampled identically so that error introduced by this method should be expressed equally among the samples. All rocks were scrapped over an enamel pan and inspected for clinging organisms. The residue was then passed through a 360 $\mu$  mesh nylon filter. This mesh retained many of the smaller Diptera and Hydracarina but was sufficiently coarse to minimize clogging. Samples were preserved in 70% alcohol, then sorted under a dissecting microscope. Because Zelt and Clifford (1972) found that a pore size of 300 $\mu$  missed half the number of individuals, the water that had passed through the filter also was examined under the microscope. The number of organisms found, however, was minimal (less than 1% of the total sample). Perhaps Zelt and Clifford (1972) were examining stream communities with a smaller size distribution of individuals. Individuals were identified to genus except the Chironomidae and Hydracarina which were further separated into "taxa" based on morphological differences which may not have paralleled the taxonomic system.

Rock area was determined by painting several layers of rubber latex over the entire rock surface (see Calow, 1972 and Dahl, 1973 for other approaches). After drying for 24 hours, the molds were peeled from the rocks, spread over a sheet of paper, and outlined. Resulting paper cut-outs were weighed to the nearest 0.001 gm. Area was calculated using a simple equation relating paper weight to area. Rock area ranged from 31.91 to 1000.30 cm<sup>2</sup>. The total collection of rocks was arbitrarily divided into three size classes based on area. Any rock with an area < 75 cm<sup>2</sup> was called SMALL, between 75 and 200 cm<sup>2</sup> was labeled MEDIUM, and > 200 cm<sup>2</sup> was labeled LARGE.

Rock complexity was defined as the degree of physical distortion in the surface. Complex rocks had a variety of smooth and creviced patches, while simple rocks were composed (almost entirely) of smooth areas. Rock complexity was measured in the following two ways:

1) All latex molds were comparatively rated on a scale of 1 to 6. Rocks with a rating of 1 or 2 were called SIMPLE. A rating of 1 indicated a rock with an entirely smooth, even surface while a rock surface with a rating of 2 had a smooth surface with shallow dips or depressions. Dark \* basaltic rocks were commonly found with this kind of surface. Rocks with a rating of 3 or 4 were termed MODERATE. These rocks had smooth surfaces with thin hairline cracks; rocks rated at 4 had several of these cracks while rocks with a rating of 3 had one or two cracks. Polished limestone \* was typically found in this condition. Rocks with a rating of 5 or 6 were called COMPLEX and had a variety of deep creviced areas and smooth patches. The highest rated rocks often had crevices or pores extending half the diameter of the entire rock. The three terms (e.g. SIMPLE, MODERATE, and COMPLEX) were convenient in broadly subdividing the total sample into size classes; ratings were required for regression analyses.

\* 2) An index was constructed comparing actual surface area (estimated from the rubber latex molds) with theoretical spherical area. Theoretical spherical area was the area of a rock if it was a perfect sphere having the same volume. Rock volume was empirically determined using water displacement. Setting the equation for the volume of a sphere to the empirically determined volume, the equation was solved for the radius. Theoretical spherical area was then estimated using the above radius in the equation for the surface area of a sphere. The ratio, actual surface

area / theoretical spherical area, was considered as a possible index for rock complexity. A Spearman rank correlation coefficient between the two complexity measures was 0.342. Although  $\rho$  was significantly greater than zero, this correlation left much to be desired. The index, actual / theoretical, was closely correlated with visual rankings only when the rocks in question were roughly spherical or egg-shaped. However, with very thin, smooth rocks, the two measures disagreed. Thin, smooth rocks have a small volume yet a large surface area, making its complexity index high. Because thin, smooth rocks were included in this sample, visual rankings (although subjective) were considered more appropriate in characterizing surface complexity. The complexity index of actual / theoretical would be useful with a collection of rocks with similar shapes. Using method 1, the entire collection could be subdivided into 9 groups based on all combinations of area and surface complexity, e.g. LARGE-COMPLEX, SMALL-SIMPLE, etc. For certain analyses, all SIMPLE, MODERATE, and COMPLEX rock communities were pooled into separate groups, with each group including all 3 size classes (e.g. SMALL-SIMPLE, MEDIUM-SIMPLE, and LARGE-SIMPLE rocks were considered as one group called SIMPLE).

Species-area curves were constructed and tested for goodness of fit by linear regression with Log area as the independent variable and species number ( $S$ ) or Log  $S$  as the dependent variable, depending upon the model. Regressions were performed separately on SIMPLE, MODERATE, and COMPLEX rock groups and on the entire collection of 48 rocks. Tests for homogeneity of slopes and elevation were made according to Zar (1974).

Before comparing slopes from the above regressions to other empirically determined and theoretically derived slopes ( $z$  values), several

assumptions implicit in Preston's (1962) slope predictions were first examined. Originally, Preston derived the following equation from his canonical hypothesis:

$$\text{Log } S = 0.263(\text{Log } J) + 0.317 \quad (1)$$

where  $J$  = number of organisms on an island,  $S$  = number of taxa on an island. Preston then assumed that  $J = \rho A$  where  $\rho$  = density of organisms per unit area and  $A$  = island area. By substituting area for number of individuals ( $J$ ), Preston found:

$$S = 1.83(\rho/m)^{.263}(A)^{.263} \quad (2)$$

where  $m$  = number of individuals in the rarest species, or in the more familiar form:

$$S = CA^{.263} \quad (3)$$

where  $C = 1.83(\rho/m)^{.263}$ .

These assumptions were made by Preston (1962):

- 1) Individuals are lognormally distributed on each of the islands.
- 2) All islands have the same population density, i.e. population size increases linearly with island area. Populations exhibit no contagion.
- 3) The series of islands considered in the species-area curve do not differ in typography, climate, elevation, etc. (i.e. the islands are ecologically equivalent).

The first assumption was examined by constructing relative abundance curves for selected rock communities. Relative abundance curves, also called dominance-diversity curves, were constructed by plotting relative abundance on the ordinate and ordered sequence of taxa from most to least abundant on the abscissa for rock communities found in the SMALL-

SIMPLE, SMALL-COMPLEX, LARGE-SIMPLE, and LARGE-COMPLEX rock groups. These groups were selected to represent extremes in rock size and complexity. Deviations from a uniform distribution (i.e. all taxa with equal abundances) for all dominance-diversity curves were tested using the Kolmogorov-Smirnov test (Pearson and Hartley, 1972). Dominance-diversity curves were compared, by inspection, to theoretical distributions such as the Lognormal and geometric distributions.

Linear relationships between population size and rock area were tested by computing a linear regression with area (A) as the independent variable and population size of the entire community on a given rock (J) as the dependent variable. The last assumption of ecological equivalency could not be assessed quantitatively from the available data, but will be addressed later.

Another set of linear regressions were computed with Log J as the independent variable and Log S as the dependent variable. This model was of the same form as Preston's equation (1). Slopes derived from these regressions could be directly compared to the theoretical predictions of 0.17 and 0.27 without the assumption of a linear increase in population size with area (m was assumed to equal 1). In this manner, the effect of a non-linearity in population size with area on the species-area slope was assessed by comparing Log S - Log A and Log S - Log J regressions.

The effect of surface complexity on species-area curves was detected by comparing slopes and elevations of the Log S - Log A regressions computed for each complexity class. Additionally, a multiple linear regression was computed with Log A and the complexity ratings as the independent variables to determine the percentage of variation in taxa number

explained by each of the variables. A forward stepwise regression was computed to develop the best empirical model for predicting rock community taxa number.

Similarity in types of taxa was considered as a measure of community structure and as a possible indicator of the effect of complexity on community structure. Taxa overlap, calculated as the percentage of taxa in common between two pooled samples, was used in comparing similar communities (i.e. communities found on rocks of similar area and complexity). Overlap values were calculated between all pairs of communities within each rock group. Overlap values were also used to contrast taxa composition among SIMPLE, MODERATE, and COMPLEX communities belonging to the same size class.

Overlap values, however, sacrificed the available information on relative abundances. Therefore, a second effect of surface complexity on structure was examined by calculating the Coefficient of Similarity (B) proposed by Pinkham and Pearson (1976) which included not only taxa identities but also their relative abundances. B values were determined by:

$$B = (1/k) \sum \frac{\text{MIN } (m_{ia} , m_{ib})}{\text{MAX } (m_{ia} , m_{ib})}$$

where  $k$  = number of different taxa in both samples combined,  $m_{ia}$  = an importance measure of the  $i^{\text{th}}$  taxon in sample A, and  $m_{ib}$  = an importance measure of the  $i^{\text{th}}$  taxon in sample B. Relative abundance and presence-absence data served as importance measures. By scoring taxa as present (=1) or absent (=0), relative abundance was held constant enabling

a comparison of taxa composition (actually, this simply reduces to a measure of taxa overlap).  $B_0$  values were computed with presence-absence data while  $B_1$  values were computed with relative abundance data. Third, individual taxa populations (number of individuals belonging to a certain taxon) were tested for significant responses (increasing or decreasing population size) to increasing rock area and surface complexity by simple and multiple linear regressions.

A priori, all statistical tests were considered significant at an of 0.10. Simple and multiple linear regressions were computed with the aid of the Statistical Analysis System (Barr et. al., 1976).

## PART I

### RESULTS AND DISCUSSION

#### Taxa-Area Relationship

Taxa numbers increased with area; from a low of 7 taxa on a rock with an area of 35.91 cm<sup>2</sup> to a high of 35 taxa on a rock with an area of 1000.30 cm<sup>2</sup>. Regression models provided a good description of this relationship. Separate S-Log A regressions for each complexity class and for the pooled data provided only a slightly better model than Log S-Log A regression models (Table 1 and Figures 1 and 2).

Diamond and Mayr (1976) discussed exponential and power function fits to species-area data from a theoretical viewpoint (also see May, 1975). Briefly, a good fit to an exponential model implied that the islands in question did not behave as isolated universes (after Preston, 1962). Rather, these islands resembled a "nested set of areas on a single landmass" where species not well adapted were nevertheless supported by immigration from outside areas, i.e. barriers to immigration were minimal. Stream rock communities, having high immigration and invasion rates (determined quantitatively in Part II), resembled nested sets of area within a single riffle. In contrast, for true islands (Preston's true islands also called isolated universes), considerable isolation from the immigration pool will keep immigration low and, according to Diamond and Mayr (1976), will produce a species-area curve conforming to the power function. My results did not support their hypothesis; both exponential and power function regression models fit, approximately as well (Table 1). Curvilinearity in Diamond and Mayr's Log S-Log A curve (Diamond and Mayr,

Table 1. Power and exponential functions: taxa-area regression models with S = taxa number and A = rock area (cm<sup>2</sup>).

## POWER FUNCTION

Rock Group	General Equation	F	P>F	r <sup>2</sup>	90% C. I. on slope
SIMPLE	Log S = 0.416(Log A) + 0.285	35.48	0.0001	0.628	± 0.120
MODERATE	Log S = 0.305(Log A) + 0.614	26.28	0.0003	0.705	± 0.107
COMPLEX	Log S = 0.269(Log A) + 0.817	44.73	0.0001	0.817	± 0.073
POOLED	Log S = 0.352(Log A) + 0.486	60.82	0.0001	0.569	± 0.076

Homogeneity of Slopes Test: F = 1.501, Not Significant

Homogeneity of Elevations Test: F = 9.379, Significant

Multiple Range Test: COMPLEX communities significantly different from other communities

## EXPONENTIAL FUNCTION

Rock Group	General Equation	F	P>F	r <sup>2</sup>	90% C.I. on slope
SIMPLE	Log S = 15.013(Log A) - 15.669	33.99	0.0001	0.618	± 4.432
MODERATE	Log S = 11.945(Log A) - 6.695	30.58	0.0002	0.735	± 3.876
COMPLEX	Log S = 14.572(Log A) - 8.786	65.68	0.0001	0.868	± 3.258
POOLED	Log S = 14.726(Log A) - 2.820	76.96	0.0001	0.626	± 2.820

Homogeneity of Slopes Test: F = 0.284, Not Significant

Homogeneity of Elevations Test: F = 10.511, Not Significant

Multiple Range Test: COMPLEX communities significantly different from other communities

Figure 1. Relationship between taxa diversity (S) and Log area (A) for SIMPLE (s), MODERATE (m), and COMPLEX (c) rock communities collected in Sinking Creek, Virginia on September 18, 1976. Regression models and supporting statistics can be found in Table 1.

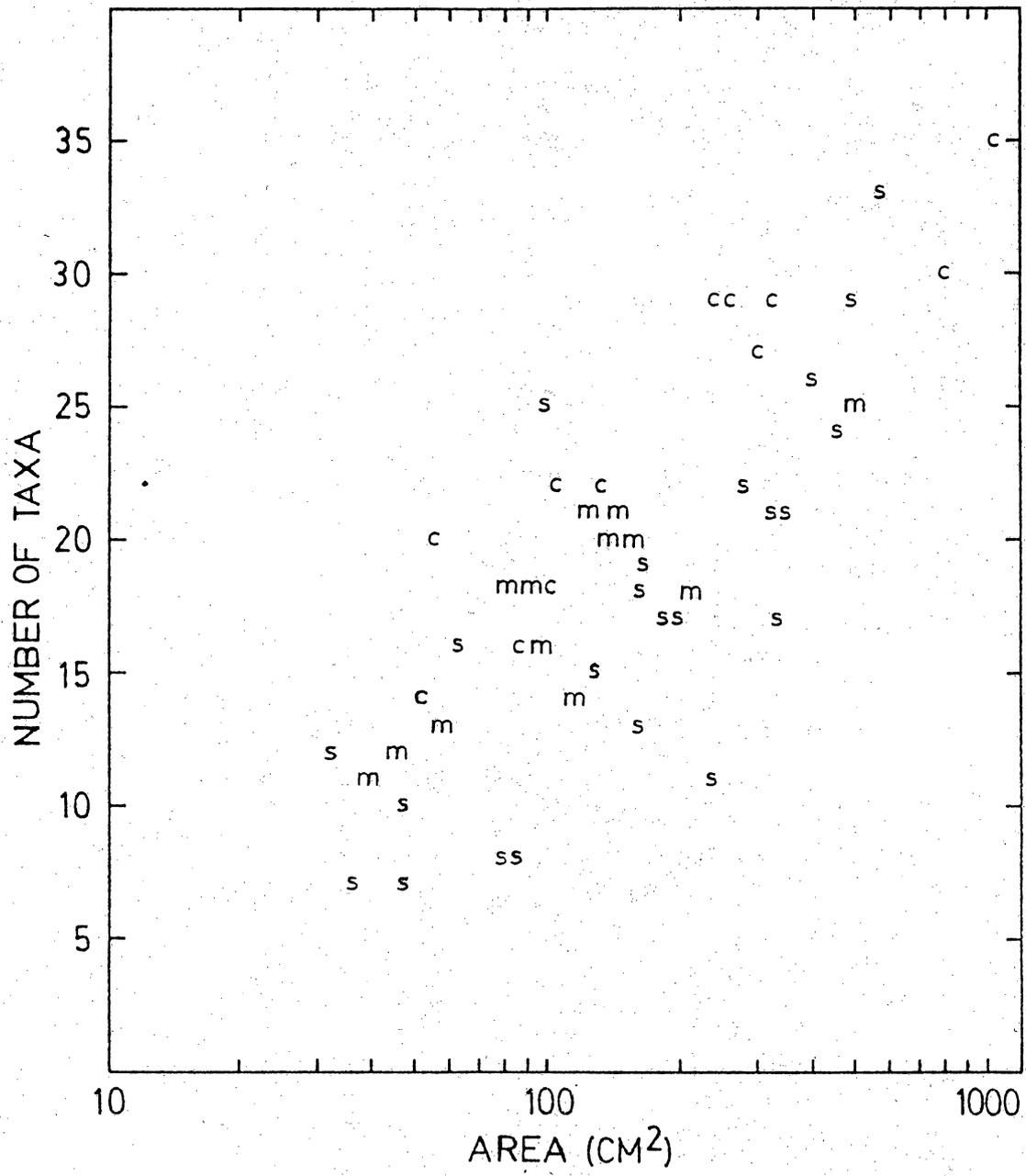
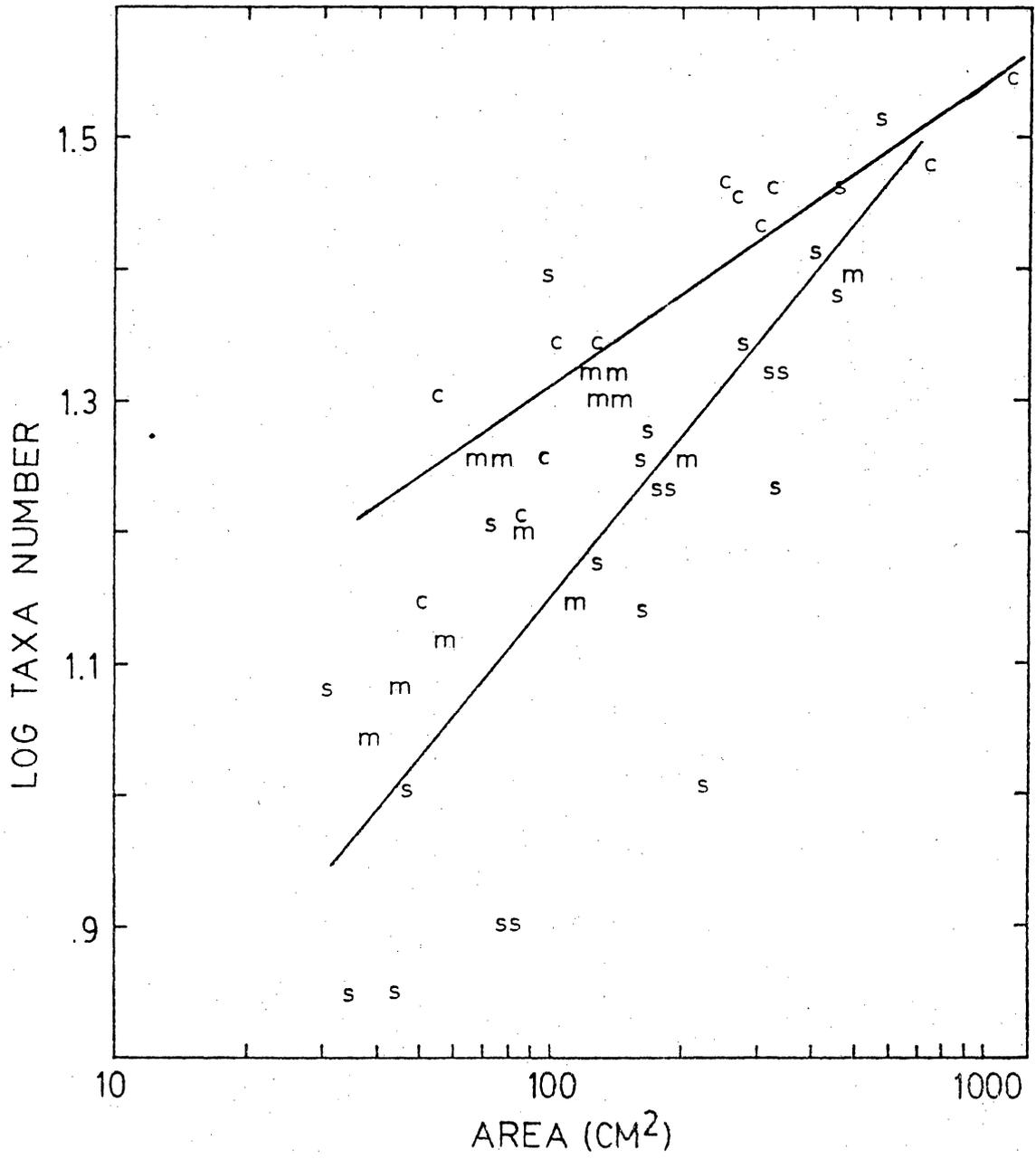


Figure 2. Relationship between Log taxa diversity (S) and Log area (A) for SIMPLE (s), MODERATE (m), and COMPLEX (c) rock communities collected in Sinking Creek, Virginia on September 18, 1976. Regression models and supporting statistics can be found in Table 1.



1976, Figure 2, p.265) at small island areas was typical of true island species-area relationships (May, 1975) and not unique to nested islands. Therefore, for the remainder of this study, taxa-area relationships will be interpreted as a power function.

Slopes ( $z$  values) for all complexity classes regressed separately and pooled (Table 1) were much higher than Preston's (1962) predicted slope of 0.27 for true islands. Several factors could have affected the  $z$  values. Three assumptions by which Preston (1962) formulated his slope predictions were not rigorously satisfied by stream data. In going from a species-individuals relationship (equation 1) to a species-area relationship (equation 3), Preston assumed population size to increase linearly with island area (i.e.  $\rho$  is constant for all islands). A Log J-Log A regression model for pooled data adequately described this relationship (Table 2); a relationship that is clearly nonlinear. In order to examine the effect of a nonlinear relationship between population size and  $S$ , another regression model was tested with Log  $S$  as the dependent variable and Log  $J$  as the independent variable. By assuming  $m$  to equal 1, this model has the same form as equation 1. The slope value should remain constant (in comparison to a Log  $S$ -Log  $A$  regression) if  $J$  were linearly related to area. Slope values generally increased (Table 3), though the increase was small. Only communities on MODERATE rocks, which had the poorest Log  $S$ -Log  $J$  regression fit, decreased slightly. Therefore, nonlinearity in the relationship of  $J$  to  $A$  was not the principle cause for the high  $z$  values, but did cause variability in estimated slopes.

Density (individuals /  $\text{cm}^2$ ) decreased with area, because slopes in the Log  $A$ -Log  $J$  regression model were less than unity (Table 2). This

Table 2. Power function: population size - rock area regression model with  $J$  = population size of an entire community and  $A$  = rock area ( $\text{cm}^2$ ).

Rock Group	General Equation	F	P>F	$r^2$	90% C.I. on slope
SIMPLE	$\text{Log } A = 0.879(\text{Log } J) + 0.110$	46.33	0.0001	0.688	$\pm 0.222$
MODERATE	$\text{Log } A = 0.719(\text{Log } J) + 0.511$	14.04	0.0032	0.561	$\pm 0.345$
COMPLEX	$\text{Log } A = 0.985(\text{Log } J) + 0.033$	40.65	0.0002	0.836	$\pm 0.281$
POOLED	$\text{Log } A = 0.844(\text{Log } J) + 0.239$	87.52	0.0001	0.665	$\pm 0.151$

Homogeneity of Slopes Test:  $F = 0.412$ , Not Significant

Homogeneity of Elevations Test:  $F = 1.878$ , Not Significant

Table 3. Power function: population size- taxa number regression model with J = population size of an entire community and S = taxa number of a community.

Rock Group	General Equation	F	P>F	r <sup>2</sup>	90% C.I. on slope
SIMPLE	Log S = 0.464(Log J) +0.252	150.31	0.0001	0.877	+ 0.065
MODERATE	Log S = 0.294(Log J) +0.653	16.83	0.0018	0.605	+ 0.129
COMPLEX	Log S = 0.332(Log J) +0.632	60.45	0.0001	0.883	+ 0.078
POOLED	Log S = 0.418(Log J) +0.385	149.67	0.0001	0.773	+ 0.057

Homogeneity of Slopes Test: Not Significant

Homogeneity of Elevations Test: Not Significant

agreed with other studies (see Lium, 1974 and Kovalek, 1978 for additional comments and discussion).

A second assumption is that of lognormality (preferably canonical) in the distribution of individuals among species for each community. Relative abundance curves were plotted for all communities, some of which are illustrated in Figures 3, 4, and 5. Relative abundance curves changed with increasing rock area. SMALL rocks supported communities that approximated a geometric distribution. Whittaker (1972) and May (1975) noted that this distribution was typically found when a single resource is limiting. For stream communities, space is an essential commodity which could limit macrobenthic populations. Communities on LARGE rocks approximated a lognormal distribution (Figures 4 and 5). A lognormal distribution can be a product of the Central Limit Theorem (May, 1975) or a pooling of geometrically distributed communities (Whittaker, 1972). May (1975) noted that geometrically distributed communities produced lower species-area slopes than lognormally distributed communities. The shift in distribution from geometric to lognormal should cause a greater change in  $S$  with  $A$ , resulting in a steeper slope.

A final assumption to the predictions of Preston is that the islands be ecologically equivalent, the importance of which was noted by MacArthur and Wilson (1967) in the following:

"As islands become large, their topography becomes more complex, especially if they are mountainous. The result is a growing heterogeneity of habitats, each of which can support ensembles of species that are ecologically semi-independent of each other. As a result, not only is the total number of individuals increasing and advancing the number of species in the expected canonical manner, but in addition the island as a whole is breaking up into multiple "semi-islands,"... The result is an en-

Figure 3. Dominance - diversity relationships for communities on SMALL-SIMPLE (A) rocks and SMALL-COMPLEX (B) rocks (each lettered symbol denotes a community).

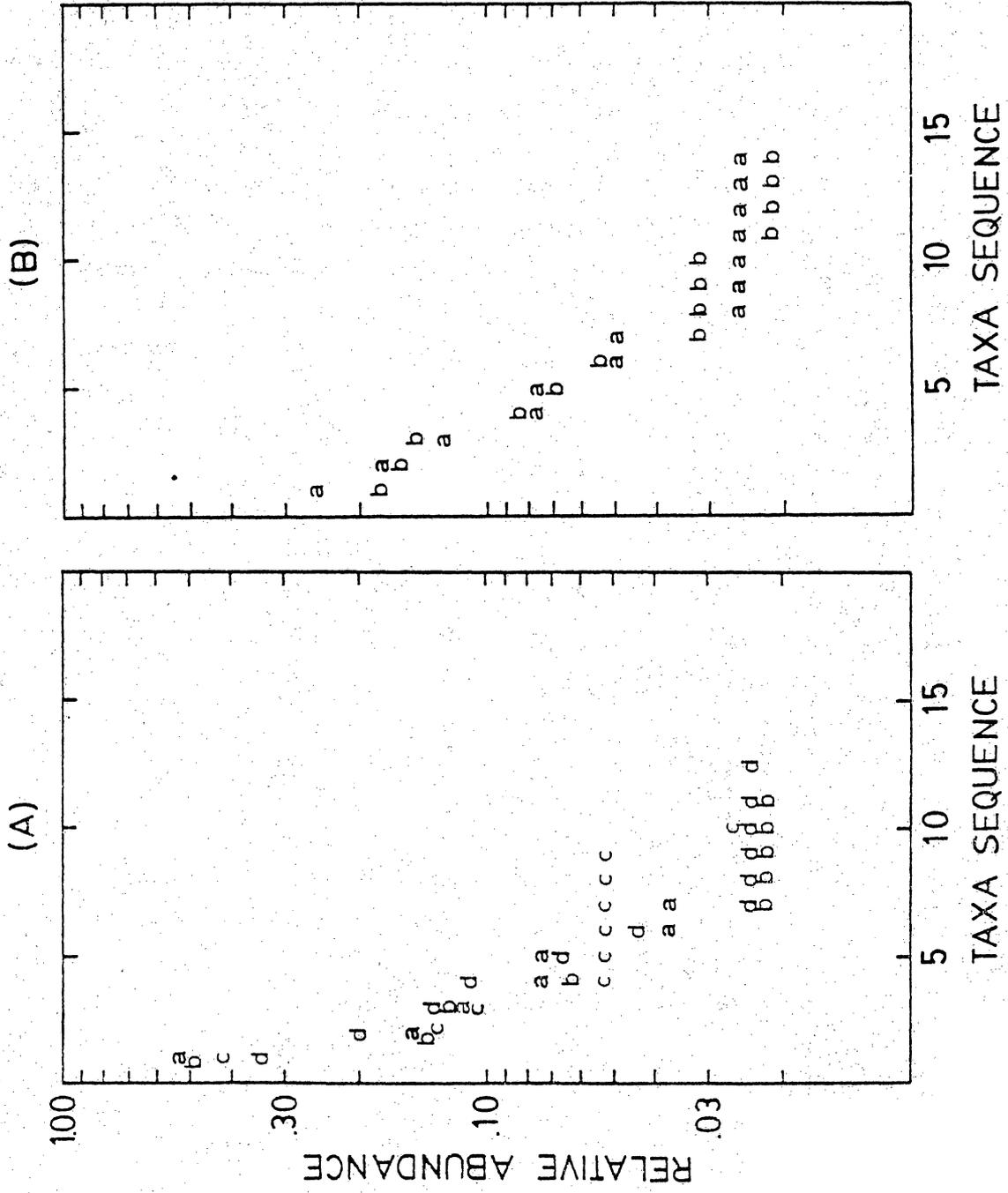
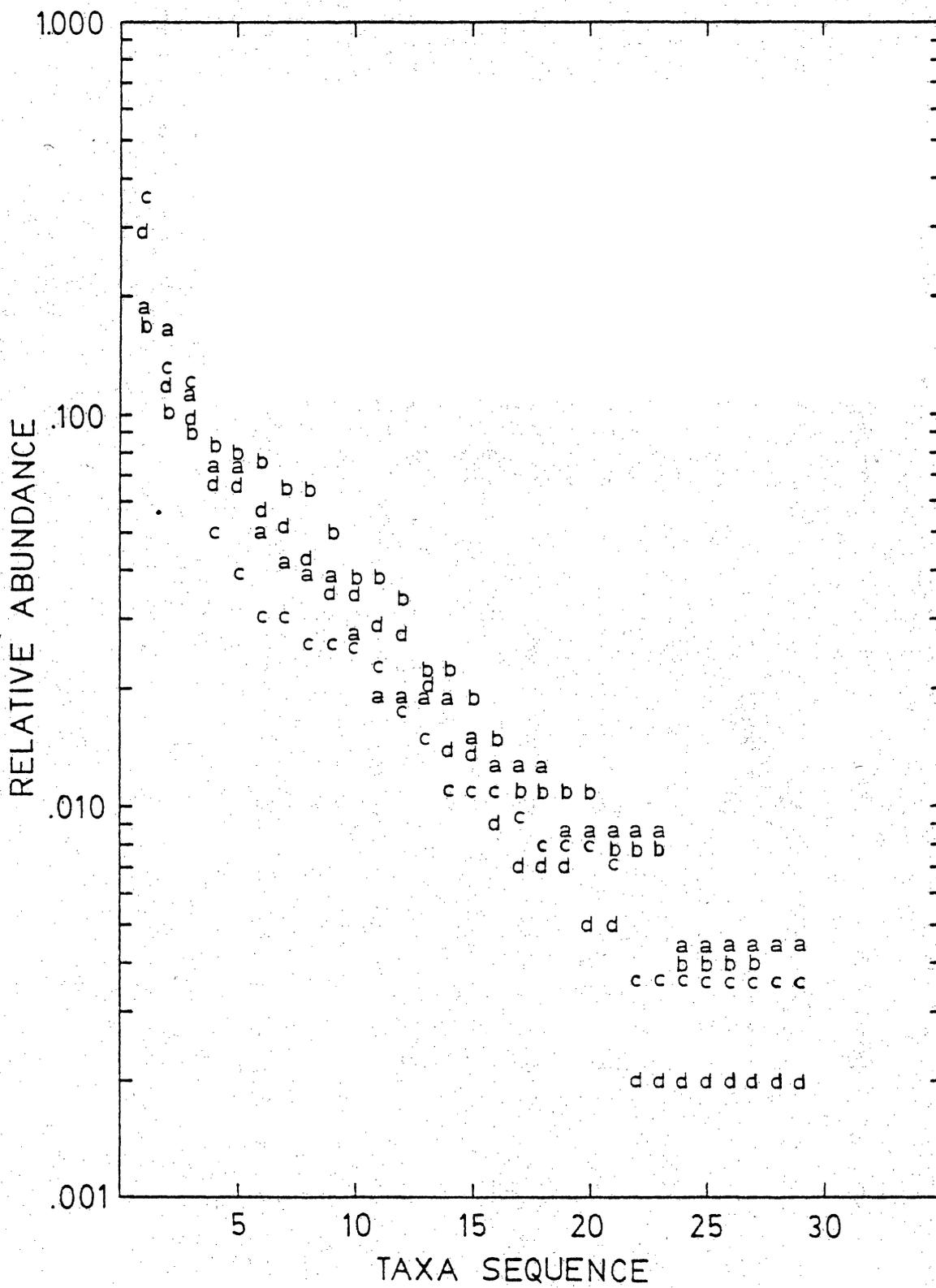


Figure 4. Dominance - diversity relationships for communities on LARGE-SIMPLE rocks (each lettered symbol denotes a community).



Figure 5. Dominance - diversity relationships for communities on LARGE-COMPLEX rocks (each lettered symbol denotes a community).



hancement of species accumulation that will account for some, and perhaps most, of the observed increment of insular  $z$  values above the predicted number."

An important question, therefore, is whether stream rocks increase in habitat heterogeneity with increasing area. This question will be examined in the next section.

#### Surface Complexity Effects on the Taxa-Area Relationship

I originally hypothesized that surface complexity could be a partial indicator of habitat heterogeneity. By separating the data into three complexity classes, the  $r^2$  for each taxa number-area regression was improved over the pooled  $r^2$  (Table 1). A multiple regression including Log A and complexity as the independent variables and Log S as the dependent variable resulted in an  $r^2$  of 0.700; a 13% improvement over the simple regression with Log A as the independent variable. Surface complexity, therefore, does affect taxa number.

Communities on COMPLEX rocks had greater numbers of taxa than communities on SIMPLE or MODERATE rocks (homogeneity test on elevation, Table 1) for any given area except the largest rocks where taxa number converged for communities on all three types of surface complexities (Figure 2). Higher taxa number was not the result of greater population densities because communities found on rocks of similar area but differing surface complexity did not have significantly different population densities (homogeneity test for elevation and slope, Table 2).

A potential modifying factor of the complexity effect on taxa number was the presence of algae. All LARGE and MEDIUM rocks had substantial algal populations, frequently with mats 1 mm thick. SMALL rocks were

variably covered, especially the SMALL-SIMPLE communities whose surfaces ranged from even coatings to only a few scattered patches. An important advantage of a complex surface is the provision of physical habitats sheltered from the current. Algae, by covering major portions (up to roughly 80% of the upper surface) of SIMPLE, MODERATE, and COMPLEX rocks in dense algal mats (with the exceptions as already noted), made all surfaces, regardless of complexity, more similar. The finding that complex surfaces still supported more taxa suggested that crevices function as more than just a haven from stream currents. Eddies, produced by crevices, can keep small patches of substrate free from thick algal colonization. These patches create microhabitats for Simulium, Psephenus, and possibly Epeorus. Crevices would also allow net-spinning trichopterans to select construction sites from a range of velocities and topographies. Dead water areas in crevices had small pools of detritus which could have been an alternate food source. Antocha was found wedged in small crevices under algal mats; presumably a thigmotactic response. All the above supports the concept that surface complexity can be an indirect measure of habitat heterogeneity and that greater complexity supports more taxa.

Surface complexity also affected the rate of change in S with A. Though a homogeneity test indicated that the difference in slopes among the three complexity classes was not significant at the 0.10 level of error (Table 1), a trend was obvious; decreasing surface complexity resulted in an increasing rate of change in taxa numbers with increasing area. This was the first indication that Preston's third assumption of ecologically constant islands may not be valid for stream rock islands even though the data were subdivided into complexity classes. Changing

rates of microhabitat availability with increasing area for each complexity class may underlie differences in slopes.

In examining two COMPLEX rocks, one LARGE and one SMALL, it was difficult to distinguish unique types of structural spatial variation found only in the LARGE rock. Such features as pores, mild ridges, and sharp right angle crevices were common to LARGE and SMALL rocks alike (though subtle changes in spatial variation may have remained undetected). However, when examining two SIMPLE rocks, the LARGE one had several distinct structural features not found on the SMALL rock. In other words, it was easy to find SMALL-SIMPLE rocks with very smooth uniform surfaces, but difficult to find LARGE-SIMPLE rocks without some structural variation (e.g. several small crevices). A series of COMPLEX rocks, grading from small to large, would exhibit little change in types of structural surface variations and, therefore, provide for a small increase in microhabitat richness with increasing area. Most increases in taxa number for the COMPLEX series would be the result of a gradual increase in microhabitat abundance, of microhabitats already found on all sizes of COMPLEX rocks. As each microhabitat becomes more abundant with increasing area, the probability of a species' extinction would decrease (by supporting more individuals of a species and reducing the chance of random extinction) resulting in an overall increase in taxa number for the entire community. For a series of SIMPLE rocks, there also would be an expected greater increase in microhabitat abundance. In addition, there would be an expected greater increase in microhabitat richness due to an increasing occurrence of structural variation on SIMPLE rocks of progressively greater area. Potentials for change in community taxa number would be greater through

the SIMPLE rock series as a result of concurrent increases in microhabitat richness and abundance. This potential should be realized in a steeper taxa-area slope.

The idea that species-area slopes are influenced by the complexity of the islands being examined may be found in other research (originally, briefly discussed in MacArthur and Wilson , 1967). Harner and Harper (1976) summed up this idea by stating, "The slope of the species-area curve or z-value is largely controlled by environmental heterogeneity. When species occur in small, discrete habitats, a higher z-value results because new species are added with each successive increase in area." Seifert (1975) found a steeper species-area slope in Heliconia inflorescences with staggered blooming. Clumps with staggered blossoms could provide a greater variety of potential microhabitats than uniform clumps, creating the potential for a more rapid increase in species diversity. Lassen (1975) found that snail diversities converged for large eutrophic and oligotrophic lakes, however, the species-area slope was steeper for oligotrophic lakes. Lassen (1975) noted that "when going from very small to somewhat larger ponds a number of new habitats are added; above a certain size of waters only a quantitative increase in pre-existing habitat types is found." Perhaps oligotrophic lakes gradually become more complex over a wide range of lake sizes, while eutrophic lakes rapidly reach a high level of complexity up to a certain size and then level off in complexity. Possible gradual increases in complexity with size would generate a faster rate of increase in types of microhabitats and produce steeper species-area slopes for oligotrophic lakes. Christiansen and Fenchel (1977) interpreted Lassen's steeper oligotrophic slope as the result of

greater extinction due to less dense populations. Again, taking one step closer to the original cause, less dense populations indicate a paucity in favorable microhabitats.

Changes in slope with complexity suggest an application of colonization to the assessment of stress on stream ecosystems. Species-area curves for more eutrophic streams should have shallower slopes and higher intercepts; based on the assumption that more eutrophic stream communities should be dominated by broadly "stress resistant" species, having greater absolute and relative abundances. Oligotrophic streams have many species of low abundance as Patrick (1972) noted, "For example, in an oligotrophic stream, where the nutrient level is very low, one typically finds many species with extremely small populations. It takes a longer time to sample an oligotrophic stream adequately than a highly nutrient rich or eutrophic stream because it is easy to overlook species with very small populations." With a random sample of rocks (including all sizes and complexities) from a shallow, fast-moving riffle, more eutrophic stream communities would initially accumulate new species at a much faster rate (number of new taxa /  $\text{cm}^2$  of rock surface sampled) than oligotrophic streams. After a large sample had been collected (surface area of about 30 rocks) the number of taxa encountered might be expected to reach an asymptote, while in an oligotrophic stream, each added sample would still encounter new taxa. Cumulative species-area curves for eutrophic streams would be more convex with an initial rapid rise in S but then a gradual approach to an asymptote. In contrast, the same curve for oligotrophic streams should increase steadily in S, even after the same cumulative area where the eutrophic cumulative curve began its asymptotic behavior.

The above curves are dependent upon the distributions of individuals among species. If stress does not alter relative abundance patterns, cumulative species or species-area curves, above and below a point source of pollution, should exhibit little difference in shape.

#### An Empirical Model for Predicting Taxa Number

Complexity, population size, and rock area were entered into a stepwise regression model to develop the best model for predicting taxa number (Appendix I). A combination of Log J and complexity provided the best model with an  $r^2$  of 0.836. Area did not provide a significant improvement to this two variable model.

#### Three Potential Surface Complexity Effects on Community Structure

Presence or absence of most taxa was not limited by any specific surface complexity. In examining two extremes of complexity, communities on SIMPLE and COMPLEX rocks, pooled, had similar taxa compositions (Table 4). With a 76.3% overlap in common taxa, there were only 14 non-overlapping taxa. These taxa, however, were represented by a total of only 27 individuals (0.37% of the total number of individuals).

Similarity in taxa composition was calculated with the Coefficient of Similarity (Pinkham and Pearson, 1976) among macroinvertebrate communities found on rocks of similar size and complexity. Utilizing presence-absence data, coefficients consistently averaged between 30 and 60% (Appendix II). Chironomid and Baetis larvae were the dominants in all communities regardless of rock size or complexity. Most discrepancies in

overlap were due to rare taxa (those taxa with low abundances of one or two individuals). Though rare taxa were regular features of each community, they varied considerably as to which taxa were present on any given community. Communities found on larger rocks had slightly higher coefficients. However, this may only be a result of sample size. Large communities, having more taxa, have less chance of differing than small communities with fewer taxa. No trend of increasing or decreasing similarity in taxa composition with complexity was found. Coefficients calculated with relative abundance data were approximately twice as low as coefficients calculated from presence-absence data (Appendix II). This again indicated the patchiness in taxa abundances found in other analyses.

In Table 4, average densities for all taxa (number of individuals /  $\text{cm}^2$ ) were computed for communities on SMALL, MEDIUM, and LARGE rocks. These densities were compared within rock size classes to see if COMPLEX communities had greater densities for each taxon than SIMPLE communities. A very simple measure was employed. The number of taxa with higher densities on COMPLEX rock communities was divided by the total number of taxa compared between SIMPLE and COMPLEX communities for each size class. For all three size classes, the percentage of taxa with higher densities on COMPLEX communities was 50% (actual percentages were 50, 58, and 49% for communities on SMALL, MEDIUM, and LARGE communities, respectively). Because approximately one half of the taxa were more dense on COMPLEX communities, one can conclude that densities, on a comparative basis between common taxa, were not lower on SIMPLE communities.

The third possible effect of surface complexity was a test of evenness. If structural variations in the environment encourage greater re-

Table 4. Average densities (number of individuals / cm<sup>2</sup>) for all taxa found on SIMPLE and COMPLEX rocks.

Taxon	SMALL/ SIMPLE	MEDIUM/ SIMPLE	LARGE/ SIMPLE	SMALL/ COMPLEX	MEDIUM/ COMPLEX	LARGE/ COMPLEX
Ephemeroptera						
Baetidae						
<u>Baetis</u>	0.243	0.073	0.122	0.252	0.178	0.071
<u>Centroptilum</u>	0.013	0.016	0.023	0.028	0.038	0.025
<u>Ephemerella</u>	...	0.003	0.001	...	...	0.001
<u>Isonychia</u>	0.018	0.010	0.016	0.009	0.010	0.018
<u>Tricorythodes</u>	...	...	0.001	...	...	0.001
Heptageniidae						
<u>Cinygma</u>	...	...	0.001	...	...	...
<u>Epeorus</u>	0.062	0.029	0.032	0.037	0.012	0.003
<u>Heptagenia</u>	0.009	0.009	0.008	...	0.002	0.008
<u>Stenonema</u>	0.036	0.014	0.027	0.028	0.012	0.027
Trichoptera						
Hydropsychidae						
<u>Cheumatopsyche</u>	...	0.004	0.001	...	...	0.001
<u>Hydropsyche</u>	0.044	0.007	0.014	0.009	0.033	0.037
Hydroptilidae						
<u>Leucotrichia</u>	...	...	0.002	...	...	0.001
Other Hydroptilidae	0.004	0.001	0.005	...	...	0.002
Philopotamidae						
<u>Chimarra</u>	...	...	0.001	...	...	0.001
<u>Wormaldia</u>	0.027	0.024	0.027	0.131	0.045	0.037
Rhyacophilidae						
<u>Glossosoma</u>	...	...	0.001	...	0.002	0.001
<u>Rhyacophila</u>	...	...	0.006	0.009	0.009	0.011
Leptoceridae						
<u>Anthrripsodes</u>	...	...	...	...	...	0.001
<u>Triaenodes</u>	...	...	0.001	...	...	0.001

Table 4 (Cont.). Average densities (number of individuals / cm<sup>2</sup>) for all taxa found on SIMPLE and COMPLEX rocks.

Taxon	SMALL/ SIMPLE	MEDIUM/ SIMPLE	LARGE/ SIMPLE	SMALL/ COMPLEX	MEDIUM/ COMPLEX	LARGE/ COMPLEX
Limnephilidae						
<u>Neophylax</u>	...	...	0.001	...	...	...
Plecoptera						
Nemouridae						
<u>Taeniopteryx</u>	...	...	...	...	...	0.001
Perlidae						
<u>Neoperla</u>	...	0.001	0.004	...	0.001	0.005
Coleoptera						
Elmidae						
<u>Optioservus</u>	0.005	0.001	0.001	...	0.007	0.006
<u>Promoesia</u>	...	...	...	...	...	0.001
<u>Stenelmis</u>	0.004	...	0.009	0.009	0.010	0.003
Psephenidae						
<u>Eubrianax</u>	...	...	0.001	...	...	0.001
<u>Psephenus</u>	0.031	0.009	0.002	0.009	...	0.001
Diptera						
Blephariceridae						
<u>Blepharicera</u>	...	...	0.001	...	...	...
Chironomidae						
15 Taxa	0.525	0.360	0.319	0.402	0.252	0.216
Rhagionidae						
<u>Atherix</u>	0.004	0.004	0.007	0.028	0.019	0.006
Simuliidae						
<u>Simulium</u>	0.027	0.016	0.007	0.028	0.007	0.008
Tipulidae						
<u>Antocha</u>	...	0.011	0.033	0.065	0.017	0.045

Table 4 (Cont.). Average densities (number of individuals / cm<sup>2</sup>) for all taxa found on SIMPLE and COMPLEX rocks.

Taxon	SMALL/ SIMPLE	MEDIUM/ SIMPLE	LARGE/ SIMPLE	SMALL/ COMPLEX	MEDIUM/ COMPLEX	LARGE/ COMPLEX
Acari						
Hydracarina						
14 Taxa	0.040	0.019	0.022	0.178	0.183	0.063
Oligochaetae	...	...	0.009	0.009	0.007	0.004
Mollusca						
Ancylidae						
<u>Ferrisia</u>	...	0.006	0.005	...	...	0.001
Pleuroceridae						
<u>Goniobasis</u>	0.004	...	0.004	...	0.007	0.002
<u>Nitocris</u>	0.013	0.010	0.014	0.009	0.017	0.011

source partitioning among species (as discussed in Smith, 1972), I hypothesized that a more even distribution of individuals among species would be expected for COMPLEX communities because greater resource partitioning decreases the percentage of resource available to any one (or several) species. For example, a rock with a very smooth surface would be ideal for Simulium and Blepharicera. The resource (space) would be primarily shared among these two taxa. Other taxa marginally adapted for smooth surfaces would utilize a small percentage of the total space. Such a community would exhibit extreme dominance. If half the rock could be made complex, the percentage of space available to Simulium and Blepharicera would decrease while the marginal taxa would increase their utilization of the total space. This would make the abundances of Simulium, Blepharicera, and the marginal taxa more equal.

Kolmogorov-Smirnov tests (Pearson and Hartley, 1972) were employed to explore the hypothesis that COMPLEX rock surfaces support a more even distribution of individuals among taxa (see Pielou, 1975, for comments on Kolmogorov-Smirnov testing). In this test, the cumulative relative abundance curve for each rock community was compared to its own theoretical curve representing maximum evenness (i.e. a curve generated by assigning the same number of individuals to all taxa in the community). The maximum evenness curve (a uniform distribution) is a straight line with a slope equal to one divided by the total number of taxa in the community. Because the Kolmogorov-Smirnov test is a function of the greatest vertical distance between two cumulative distributions, cumulative abundance curves which deviate more from the uniform distribution will have larger Kolmogorov-Smirnov statistics. This statistic, therefore, can serve as a measure for

evenness. COMPLEX communities should, if their taxa are distributed more evenly, have smaller distances than SIMPLE communities.

A Kruskal-Wallis test with each combination of size and complexity serving as a treatment was significant at  $\alpha = 0.17$ . The result, though not significant at the a priori level of  $\alpha = 0.10$ , indicated that more intensive sampling could reveal significant trends in non-uniformity of relative abundance distribution with rock complexity.

#### Effect of Area and Surface Complexity on Selected Taxa

Simberloff (1972) proposed a direct effect of area on species number; smaller islands support smaller populations of each species, increasing the chance of species extinction on smaller islands. A necessary prerequisite for Simberloff's hypothesis, therefore, is the documentation of a possible trend in increasing taxon population size with increasing area. Linear regressions were performed on all taxa occurring on 10 or more communities (Table 5). Additionally, to examine the effect of area and surface complexity together, multiple regressions including area and complexity as the independent variables were also calculated (Table 5).

Of the 30 taxa examined, 50% exhibited significantly increasing population sizes with increasing rock area. These included all the Chironomidae, Neoperla, most ephemeropterans, two net-spinning Trichoptera, Simulium, Antocha, and Nitocris. With greater sample sizes it seems very likely that many other taxa would exhibit significant population size-area relationships because all taxa with 28 or more appearances exhibited significant effects of some kind. No taxa populations were inversely related to rock area.

Table 5. Population size - area regression models for taxa found on 10 or more rock macroinvertebrate communities (\*...negative slope estimate).

Taxon	Single Regression: Area		Multiple Regression: Area and Complexity				n
	r <sup>2</sup>	P>F	r <sup>2</sup>	Area P>F	Complexity P>F	Total P>F	
Chironomid #07	0.170	0.0039	0.229	0.0052	0.0739*	0.0033	47
Chironomid #08	0.513	0.0012	0.513	0.0018	0.9484	0.0065	17
Chironomid #09	0.307	0.0001	0.307	0.0002	0.8577	0.0008	42
Chironomid #10	0.208	0.0498	0.266	0.0487	0.2034	0.0673	19
Chironomid #16	0.103	0.0278	0.217	0.0127	0.0148*	0.0045	47
<u>Baetis</u>	0.381	0.0001	0.385	0.0001	0.6235*	0.0001	48
<u>Isonychia</u>	0.184	0.0226	0.196	0.0209	0.5476*	0.0651	28
<u>Stenonema</u>	0.439	0.0001	0.447	0.0001	0.5192	0.0001	33
<u>Epeorus</u>	0.127	0.0279	0.317	0.0084	0.0036*	0.0013	38
<u>Centroptilum</u>	0.297	0.0006	0.340	0.0004	0.1534	0.0008	37
<u>Heptagenia</u>	0.035	0.3837	0.041	0.3639	0.7256*	0.6482	24
<u>Psephenus</u>	0.001	0.8922	0.006	0.9563	0.7608	0.9451	23
<u>Stenelmis</u>	0.029	0.5610	0.086	0.7078	0.4249	0.6099	14
<u>Optioservus</u>	0.072	0.2991	0.118	0.4417	0.4059	0.4156	17
<u>Neoperla</u>	0.363	0.0039	0.380	0.0050	0.4908	0.0136	21
<u>Atherix</u>	0.061	0.2154	0.066	0.2118	0.7136	0.4409	27
<u>Antocha</u>	0.431	0.0001	0.515	0.0001	0.0243	0.0001	35
<u>Simulium</u>	0.174	0.0306	0.180	0.0310	0.6629*	0.0920	27
Hydroptilidae	0.094	0.3588	0.212	0.2309	0.3069*	0.3865	11
<u>Hydropsyche</u>	0.273	0.0018	0.443	0.0017	0.0050	0.0002	33
<u>Wormaldia</u>	0.427	0.0001	0.478	0.0001	0.0613	0.0001	42
<u>Rhyacophila</u>	0.114	0.1062	0.169	0.1026	0.2518	0.1428	24
Oligochaetae	0.045	0.4301	0.110	0.6374	0.3474*	0.4686	16
<u>Nitocris</u>	0.344	0.0001	0.344	0.0001	0.9917*	0.0005	39
<u>Goniobasis</u>	0.015	0.6242	0.307	0.8474	0.0239	0.0604	18
<u>Ferrisia</u>	0.001	0.9777	0.131	0.7331	0.2749*	0.5326	12

Table 5 (Cont.). Population size - area regression models for taxa found on 10 or more rock macroinvertebrate communities (\*... negative slope estimate).

Taxon	Single Regression: Area		Multiple Regression: Area and Complexity				n
	$r^2$	P>F	$r^2$	Area P>F	Complexity P>F	Total P>F	
Hydracarina #02	0.006	0.7764	0.336	0.8080	0.0195	0.0572	17
Hydracarina #03	0.001	0.9697	0.088	0.7923*	0.1604	0.3647	25
Hydracarina #11	0.066	0.3937	0.072	0.4572	0.8109*	0.6902	13
Hydracarina #19	0.077	0.1386	0.261	0.1523	0.0151	0.0169	30

Surface complexity affected the population size of several taxa. Net-spinning trichopterans, Antocha, and Epeorus exhibited combined effects of area and complexity on population size. Only Epeorus populations decreased with increasing surface complexity (as noted by its negative slope in Table 5). Two taxa of the Hydracarina in this study and Goniobasis displayed no area-population size effects but did exhibit increasing populations on rocks of greater surface complexity. The poorly streamlined shape of the Hydracarina would presumably make survival difficult on exposed, smooth areas (though the Hydracarina are equipped with strong claws). However, thick algal mats on SIMPLE rocks should have provided adequate protection from the current. The absence of an area effect on population size was puzzling. It would seem that as more crevices appeared on larger COMPLEX rocks, the number of Hydracarina that could utilize that surface would increase. In direct contrast to Nitocris, Goniobasis populations were affected by complexity but not area. The smaller attachment surface of the foot on Goniobasis in addition to its elongate spiral shell may make it necessary for Goniobasis to seek greater protection from currents (see Dazo, 1965). This, however, does not explain the lack of an area effect on population size.

Multiple regression models of only two taxa accounted for over 50% of the variability in population size. Though many of the taxa appeared patchily distributed among the rocks (i.e. poor  $r^2$  values), the overall relationship between rock area and total community size was predictable (Table 2). This indicated a compensation effect among the members of a particular community; when one taxon occurred in low abundance others

occurred in high abundance with the net result being a fairly constant increase in total numbers with area.

PART I  
SUMMARY

A species-area relationship for stream macroinvertebrate communities on stream rocks did exist. Species-area regression slope values fell within the range for true islands rather than within the range for nested islands, even though macroinvertebrate communities resemble nested islands. The assumptions implicit in Preston's predicted  $z$  values of 0.17 and 0.27 were unrealistic when applied to stream communities. Communities on rocks were numerically small on all but the largest rocks, limiting the likelihood of a lognormal distribution to communities found only on large rocks. The number of individuals in a community did not proportionately increase with rock area. Utilizing Preston's original relationship of species number to population size, the result was the same: high  $z$  values.

Rock islands did not remain ecologically equivalent with increasing island area. Surface complexity affected the species-area curve, COMPLEX rocks supported more diverse communities. There was a progressively steeper species-area slope for less complex rock macroinvertebrate communities, indicating that, with increasing area, SIMPLE rock macroinvertebrate communities accumulate new microhabitats at a faster rate than COMPLEX or MODERATE rocks.

Other surface complexity effects on community structure were equivocal. SIMPLE and COMPLEX communities supported similar types of taxa, differing only in rare taxa. The 14 nonoverlapping taxa were represented by a total of 27 individuals (9 taxa were unique to COMPLEX communities). Population densities per community were independent of rock area, though

decreasing with increasing rock area. Similarity in taxa composition was low among SIMPLE and COMPLEX communities alike. Relative abundance distributions were similar for communities on rocks of the same size and independent of surface complexity. SMALL communities were geometrically distributed and LARGE communities were approximately lognormally distributed. All communities were numerically dominated by the Chironomidae and, to a lesser extent, by Baetis. The effect of surface complexity in determining taxa number was lessened by the presence of algal mats. These mats covered all surfaces on MEDIUM and LARGE rocks but variably on SMALL rocks (especially on SMALL-SIMPLE rocks).

Certain taxa were affected by rock area and/or surface complexity. Among others, the Chironomidae, most of the Ephemeroptera, and Simuliidae exhibited significantly increasing population sizes with increasing rock area, while two of the Hydracarina and Goniobasis were affected by surface complexity (rocks of greater complexity supported more individuals) but exhibited no area effect on population size. Taxa exhibiting both area and surface complexity effects were the net-spinning trichopterans, Antocha, and Epeorus.

PART II  
A Functional Analysis  
of  
Stream Invertebrate Colonization

INTRODUCTION

The number of species on an island at any given time is a product (an "end point") of several processes. MacArthur and Wilson (1963) proposed that island communities exist in an equilibrium with species number remaining relatively constant through time by having a balance between species immigration and extinction. They went further and postulated that although species number remains constant, actual species composition continually changes (i.e. turnover). A species equilibrium with turnover has been termed a dynamic equilibrium. Because species number fluctuated in a predictable manner with rock area and surface complexity (Part I), processes which shape communities must also be affected by area and surface complexity. Part II is an examination of the processes of colonization, immigration, extinction, and invasion which shape community structure. By monitoring artificial substrate colonization (both daily and periodically over specified time intervals) these rate processes will be assessed qualitatively and quantitatively. The influence of substrate area and complexity over the processes that determine community structure will be examined. First, however, available evidence (from the literature) concerning stream invertebrate immigration, extinction, and community equilibria will be reviewed.

### Immigration

The definition of immigrant has, in itself, been a variable in island studies (see MacArthur and Wilson, 1967, pp.64-65). MacArthur and Wilson (1967) considered immigrants to be only those species that reach an island with a potential for reproduction. For stream communities, an immigrant could be any species that makes at least momentary contact with the rock surface. However, for this study, an immigrant will be defined as any taxon reaching a given rock having a potential for successful colonization. If all taxa making momentary contact with a rock surface were considered immigrants, it would greatly inflate both immigration and extinction rates or as noted by Smith (1975), "At a ridiculous extreme every death or movement creates extinction at that exact point. Robins become extinct in an apple tree many times each day whenever they elsewhere." It was decided not to place too much importance on extreme transients (those taxa quickly emigrating upon contact with the rock surface).

An individual of a given taxon was considered a potential colonist if it remained on the surface for at least several hours (see Methods, Part II). A potential for reproduction could not be incorporated into the definition because most macrobenthic invertebrates in the rock communities were immature forms. In classical island studies (see MacArthur and Wilson, 1967), a single reproductive individual (or pair) well adapted for survival could undergo a substantial increase in population size through reproduction and insure some immunity from random extinction. In contrast, an individual of a given macroinvertebrate species perfectly adapted for survival on a certain rock surface may experience ample resources and little competition but still not increase its population size. An increase

in population size for a species would be totally dependent upon that species' frequency of occurrence in the immigration pool. The structure of immigration pools may, therefore, be very important in influencing the structure of macroinvertebrate communities (Fox, 1977).

Macroinvertebrate immigration is high, primarily due to stream drift (see Waters, 1972, for review). Denuded stream bottoms or introduced substrates are rapidly colonized (Townsend and Hildrew, 1976; Ulfstrand et. al., 1974). While downstream drift is the dominant contributor to colonization, active upstream migration and vertical migration up through the sediments may also be important (Williams and Hynes, 1976).

Several factors influence immigration. In classical oceanic island studies, distances from the pool of potential immigrants to the islands in question are an important factor in determining immigration rates. Distant islands have lower immigration rates than islands near the mainland. In contrast, distances between rocks are small, from one meter (e.g. scattered rocks in a pool) to less than a centimeter (e.g. a riffle area). Additionally, the distance traveled by a drifting individual is also small; estimated range from 2 meters to 100 meters (see Townsend and Hildrew, 1976). Thus, there should be a negligible effect on immigration. MacArthur and Wilson (1967) noted that islands of greater size might intercept more immigrants than smaller islands. The possibility of greater rock size affecting immigration rates does seem plausible and will be examined in Part II.

#### Extinction

High immigration rates are, in turn, indicative of high extinction

rates because every immigrant must have emigrated from another substrate (not necessarily a rock, however). Extinction could result from any of the following:

1) Extinction may be due to stochastic events. A predator cropping prey in a fine grained manner, the tumbling of rocks during a spate, or simply a lost grip on the substrate are all very real examples of stochastic extinction for individuals. The likelihood of extinction for a taxon would be inversely proportional to its population size because the loss of an individual from a small population would comprise a relatively large portion of that population (Simberloff, 1976).

2) Changing physical and biological conditions of the rock surface can alter habitat favorability for many taxa. For example, rapid colonization of implanted substrate trays (Ulfstrand et. al., 1974) was characterized by declining colonization rates of Simulium ornatum and a sudden increasing rate of Caenis rivulorum. During colonization, these trays were gradually filled with large amounts of detritus which may have been an important factor in habitat selection. Glime and Clemons (1973) noted that algae can be important in attracting certain invertebrates. The patchy distribution of algae on stream rocks in Sinking Creek could present different types of microhabitats to colonizing macroinvertebrates.

3) Spatial competition and other forms of intra- and interspecific competition (e.g. predation) may eliminate colonizing individuals and possibly, entire taxa. Allan (1975) concluded that there was an increase in organism interactions with colonization time. High densities of individuals during later stages of colonization could initiate behavioral and/

or density dependent drift (see Waters, 1972; Fox, 1977).

4) As shown in Part I, increased complexity resulted in higher taxa numbers. Complexity of the surface would lower extinction rates for immigrants by providing more habitats (refer to Discussion in Part I).

5) Extinction would be a consequence of basic life history patterns, because many macroinvertebrates must emigrate in order to complete emergence.

### Dynamic Equilibrium

Partial evidence supports the hypothesis that stream macroinvertebrate communities can exist in a dynamic equilibrium (whether they do, remains to be proven). Several investigators, in experimentally constructing colonization curves, found species number and abundance to become asymptotic after short colonization periods. Townsend and Hildrew (1976) found species number to stabilize for substrate trays within 3 days after implantation. Ulfstrand et. al., (1974) found a leveling of diversity ( $H'$ ) between days 15 and 30. Likewise, Dickson and Cairns (1972) found a leveling off at around day 42. All of these results suggest an approach of an equilibrium. Additional evidence can be found in Part I. The fact that a species-area curve exists, indicates that species number fluctuates about a mean species number for any given size of rock. Because rock macroinvertebrate communities are constantly exposed to drift, their rates of immigration must be offset by opposing rates of extinction.

The wide discrepancy in times to approach equilibrium for the above studies may be dependent upon the stream in which the experiment was performed. For example, in the Townsend and Hildrew (1976) study the immi-

gration pool was much smaller (approximately 10 species) than the other two studies. In this case, equilibrium should occur sooner (and it does). Sampling technique may be equally as important in determining equilibrium times. In the first two studies, trays of rocks were used while Dickson and Cairns (1972) used individual substrates. Each rock in a tray undergoes a separate approach to an equilibrium. By pooling the species found on all the rocks in a tray into a single species list, a large percentage of the total immigration pool will be encountered, shortly after implantation of the trays. Pooling gives the appearance of a rapid approach to equilibrium, while, in fact, communities on each rock may be far from reaching an equilibrium.

I have been careful, until now, not to mention dynamic equilibrium in conjunction with stream rock invertebrate communities. If data for colonization curves are collected by sacrificing subsets of "identical" trays or solitary substrates over several sampling periods, no empirical estimate of species turnover can be reliably calculated because physically similar trays or substrates (sampled at the same time) support communities that undergo independent approaches to equilibrium, making any comparison of species lists (or computation of turnover) tenuous (see Schoener, 1975). Without a technique for censusing the same rock community through time, a dynamic equilibrium cannot be experimentally verified. However, some evidence is available if one is willing to look at streams at a larger scale. Patrick (1975) found fairly constant species numbers at sampling sites, but different types of species for the Savannah River or as she noted, "the relative constancy of  $\alpha$ -diversity with geography or time conceals a high species turnover with geography or time, analogous to

high  $\beta$ -diversity." Friberg et. al.(1977) also observed the same phenomenon.

Turnover, though not readily observed for a single stream community, is extremely probable. As Smith (1975) noted in general, "Inevitably this struggle (to occupy space) involves the turnover rate in each population, since replacement in space is not necessarily by the same species." High immigration and extinction of individuals in streams must constantly create vacancies which are rapidly occupied, creating high turnover even at an equilibrium.

## PART II

### METHODS

The sampling site, a section of shallow stream riffle approximately 12 m by 11 m, was located 85 m downstream from the State Route #42 bridge on Sinking Creek. At normal discharge the depth of the riffle area was  $0.3 \pm 0.05$  m (SD) and the velocity was  $10.0 \pm 0.1$  cm/sec (SD) (45 measurements were taken of each).

Hemispherical concrete substrates (made of Ready Mix Sand Sakrete) were formed, utilizing halves of hollow metal globes as molds. Four different sizes of substrates were made with the following areas and labels:

1) Molds with a diameter of 2.222 cm ( $31 \text{ cm}^2$ ) were labeled SMALL.

2) Molds with a diameter of 4.572 cm ( $131 \text{ cm}^2$ ) were labeled

INTERMEDIATE.

3) Molds with a diameter of 6.604 cm ( $274 \text{ cm}^2$ ) were labeled MEDIUM.

4) Molds with a diameter of 12.700 cm ( $1013 \text{ cm}^2$ ) were labeled LARGE.

The use of metal globe shells as molds presented a unique opportunity in exploring surface complexity effects on community structure, independent of area. By deforming the molds (with a hammer), surface complexity was increased (crevices and folds were created) without changing area. This was done for MEDIUM substrates; Medium molds were labeled either MEDIUM-SIMPLE (undeformed) or MEDIUM-COMPLEX (deformed). In the immigration portion of this experiment, other sizes of molds were deformed in the same manner and labeled accordingly. Molds were leached for 30 days in standing water.

To construct colonization curves (number of taxa colonizing a given

substrate type through time), substrates were set on the stream bottom and were to be periodically sampled over a 40 day period (beginning on February 11, 1977). Four repetitions for each of four substrate types, SMALL-SIMPLE, MEDIUM-SIMPLE, MEDIUM-COMPLEX, and LARGE-SIMPLE, were to be sampled on Days 2, 4, 10, 20, 30, and 40. All substrates were randomly assigned positions within 12 rows aligned normal to the direction of the current. Rather than random placement within a defined area, the aligned rows aided in the anticipated difficulty in locating substrates during periods of high discharge and turbid water. Rows were spaced 2 m apart with each substrate separated by 1 m along a given row. There were 8 substrates per row giving a total of 96 substrates. Before initiation of the experiment, all substrates were assigned, at random, a time to be sampled. Concrete substrates in this colonization experiment were referred to as colonization substrates or COL-substrates.

Day 40 samples were not collected. On Day 36 an upstream sandbar shifted during a storm, scoured most Day 40 COL-substrates, and made it necessary to delete these COL-substrates from any analyses. Colonization data up through Day 30 were analyzed. Otherwise, discharge was constant (monitored by recording depth at several reference stations) except on Day 14 when stream discharge doubled, returning to normal by Day 18. Two of the LARGE-SIMPLE and one each of the MEDIUM-SIMPLE and MEDIUM-COMPLEX COL-substrates were damaged (scouring action along with displacement downstream). Interestingly, the smaller COL-substrates showed no signs of any damage. One LARGE-SIMPLE COL-substrate was lost in transport on Day 30. An unfavorable weather report (which never materialized) prompted sampling on Day 19 rather than Day 20. Sampling procedure for individual substrates

was the same as in Part I. A daily log was kept of any changes on the COL-substrates (e.g. gradual colonization by algae).

Structural characteristics of COL-substrate communities were analyzed in the same manner as in Part I. Colonization curves were described by linear regression. Also, 90% confidence intervals in mean taxa number on every sampling interval were determined for each type of COL-substrate. A species-area curve, using a power function, was calculated for Day 30 COL-substrate communities.

Another series of substrates was needed to estimate immigration. These substrates, called IMM-substrates, were sampled daily with every effort made at not damaging the gradual colonization of algae on the surfaces, except when otherwise noted. The following types of IMM-substrates were included:

- 1) MEDIUM-SIMPLE and MEDIUM-COMPLEX IMM-substrates (one each).
- 2) NEW MEDIUM-SIMPLE and NEW MEDIUM-COMPLEX IMM-substrates (one each).

These substrates were scrubbed clean of algae (with a nylon bristle brush) after each daily sampling.

- 3) INTERMEDIATE-SIMPLE and INTERMEDIATE-COMPLEX IMM-substrates (one each).
- 4) SMALL-SIMPLE #1 through #4 (a total of four).
- 5) LARGE-SIMPLE and LARGE-COMPLEX IMM-substrates (one each).
- 6) NATL-COMPLEX IMM-substrate (one). This rock, having an extremely contorted surface (1.35 times greater in area than LARGE substrates), had cross sectional profile similar to LARGE substrates.

All 13 IMM-substrates and rock were positioned 2 m downstream from the last

row of COL-substrates. In the daily sampling, each IMM-substrate was carefully lifted from the bottom and rinsed with a mild jet of water over an enamel pan (except NEW MEDIUM-SIMPLE and NEW MEDIUM-COMPLEX IMM-substrates as noted earlier). All IMM-substrates were inspected for clinging forms. After cleaning, IMM-substrates were returned to the same location. Total air exposure time did not exceed 3 minutes.

Of the four SMALL-SIMPLE IMM-substrates, only two remained intact by Day 30. During the period of high discharge, Days 14 to 17, several collection days were missed because I was unable to locate them in the turbid water (see actual days in Figure 12). Unfortunately, it was during these days that many immigrants arrived for other IMM-substrates. Thus, immigration rates over the interval, Days 11 to 19, were lower than they should have been, even after averaging over fewer days.

Daily sampling was an attempt at estimating the arrival rate of invertebrates before emmigration occurred. Recalling the definition of an immigrant as an individual which remains on the substrate for at least several hours, daily sampling of IMM-substrates did not guarantee that all collected organisms had been "residents" for the specified period of time of a few (at least) hours (pilot studies indicated that, by sampling at noon, most individuals had arrived on the substrates by early morning). Gentle rinsing of IMM-substrates so as not to disturb algal colonization was necessary for IMM-substrates to approximate the changing conditions on the COL-substrates. However, this certainly resulted in an underrepresentation in numbers of organisms (immigrants), especially later, when algal mats were thick. Even with gentle rinsings, the algal mats

were not as thick on IMM-substrates as on COL-substrates. By the daily scrubbing of NEW MEDIUM IMM-substrates, the effects of algal colonization on immigration were measured.

Cumulative immigration curves were determined for all IMM-substrates. The taxa (and their abundances) of a single day's sampling were pooled with previous day collections. This was called the immigration pool. For example, a Day 10 immigration pool was a pooling over the first 10 days of sampling. Cumulative immigration curves represented the appearance of new taxa during daily accumulations of individuals into the immigration pool for each IMM-substrate.

Several rates were determined from sampling COL- and IMM-substrates. These were defined as follows:

- 1) Colonization rate is the daily increment in taxa on COL-substrates. Because COL-substrates could not be sampled every day, increments in taxa number between two sampling dates were divided by the number of days separating the two sampling dates. Colonization rate, therefore, was assumed to be linear within any sampling interval.
- 2) Growth rate is the daily increment in number of individuals on each COL-substrate type, calculated as the average increase in number of individuals between consecutive sampling dates divided by the number of days between the sampling dates.
- 3) Immigration rate is the daily appearance of new taxa not previously found on a given IMM-substrate. The rate could be determined daily, unlike colonization rate. Additionally, immigration rates were averaged over each sampling interval.

- 4) Invasion rate is the total daily influx of all individuals onto an IMM-substrate regardless of whether an individual's taxon had previously appeared on the same IMM-substrate. Rates were averaged over each sampling interval.
- 5) Replacement rate is the total daily influx of taxa onto an IMM-substrate regardless of whether a particular taxon had previously been recorded on a given substrate.

No reliable method, except a complete monitoring of all immigrations and a continuous censusing of all colonists on the same island, can provide the necessary data to completely assess extinction. Extinction can be defined as the loss of colonizing species from an island through time. Because each community undergoes a separate approach to a dynamic equilibrium, a comparison between two communities collected on different islands (though physically identical) on different sampling dates is not comparable to censusing the same island at two different (see Schoener, 1974) times. The two techniques give different results. For example, an island that is permitted to undergo colonization for 10 days may support a community of 4 species: A, B, C, and D. Another island allowed to undergo colonization for 20 days could accumulate 6 species: A, B, C, E, F, and G. In comparing the lists we conclude that 1 species went extinct, species D. However, another island undergoing colonization for 20 days could accumulate the same number of species but different types of species (e.g., species E, F, G, H, I, and J). In this case we conclude that species A, B, C, and D went extinct. Extinction rate estimates would depend upon the 20 day island island that was chosen for comparison. Unfortunately, no techniques are fully

available for complete monitoring of all immigrations and extinctions on a single island (stream rock). Both techniques also fail to record species turnover within sampling periods.

In this study, extinction will be estimated as the difference between the immigration and colonization rates for each sampling interval. Because species turnover is likely, this method will be conservative.

PART II  
RESULTS and DISCUSSION

Colonization

Colonization was rapid with LARGE COL-substrates accumulating an average of 26.7 taxa in 30 days (Figure 6 and Table 6). A nonparametric ordered alternatives Jonckhere test (Hollander and Wolfe, 1973) with an a priori ordering of SMALL-SIMPLE, MEDIUM-SIMPLE, and LARGE-SIMPLE as treatments, indicated a significant increase in taxa number with area among the Day 30 samples. On Day 30, MEDIUM-COMPLEX COL-substrates had more taxa than MEDIUM-SIMPLE COL-substrates (Table 6).

The colonization curves were more than adequately described by a power function. Linear regressions for each type of COL-substrate with Log Day as the independent variable and Log S as the dependent variable produced significant fits (Appendix III). The intercepts differed, indicating that the curves were displaced towards a higher number of taxa for larger or more complex COL-substrate communities.

Of interest, was whether the colonization curve for any type of COL-substrate community approached an asymptote in taxa number with time. Only the LARGE-SIMPLE COL-substrate colonization curve appeared to be approaching an asymptote because the average number of taxa was similar on Days 19 and 30 (Figure 6 and Table 6)(even though the 90% confidence interval on Day 19 was tremendously large, the small sample size,  $n = 2$ , distorted the probable lower variability in S). Other Day 30 COL-substrates (SMALL-SIMPLE, MEDIUM-SIMPLE, and MEDIUM-COMPLEX) demonstrated no sign of asymptotic behavior.

Figure 6. Colonization curves for each COL-substrate community type.

(s)...SMALL-SIMPLE #3

(ms)..MEDIUM-SIMPLE

(mc)..MEDIUM-COMPLEX

(l)...LARGE-SIMPLE

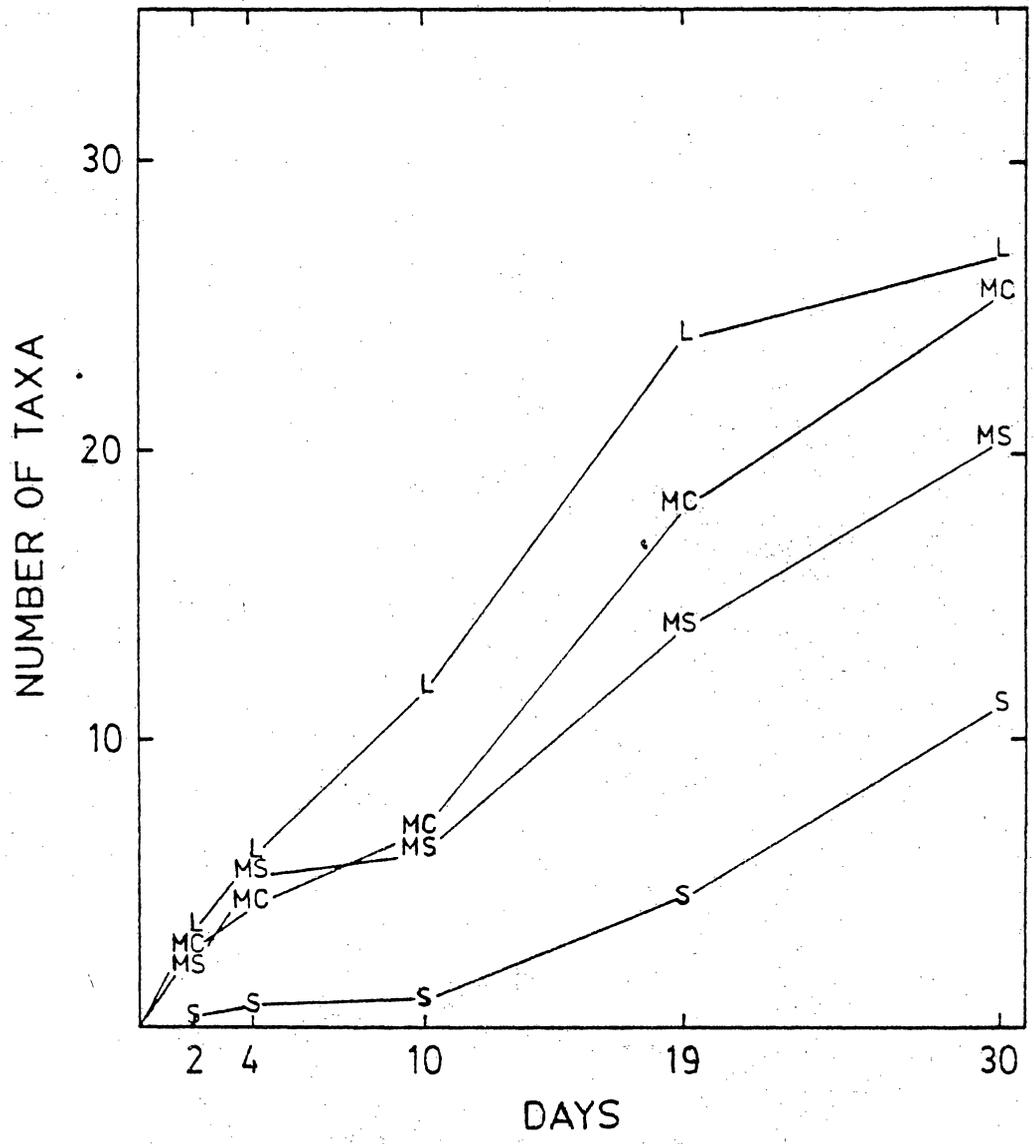


Table 6. Pertinent statistics in describing the colonization curves produced by periodic sampling of COL-substrates. Colonization is expressed as Taxa / Day.

SUBSTRATE	DAY	N	LOWER S 90% C.I.	MEAN S of TAXA	UPPER S 90% C.I.	TAXA OVERLAP	RATE COLONIZATION
SMALL/ SIMPLE	2	4	0.000	0.000	0.000	0.000	0.000
	4	4	0.162	0.750	1.338	0.000	0.375
	10	4	0.039	1.000	1.961	0.000	0.042
SIMPLE	19	4	2.981	4.500	6.019	27.681	0.389
	30	4	9.299	11.250	13.201	37.275	0.614
MEDIUM/ SIMPLE	2	4	0.462	2.500	4.538	14.883	1.250
	4	4	5.039	6.000	6.961	27.832	1.750
	10	4	3.699	6.500	9.301	53.386	0.083
SIMPLE	19	3	10.628	14.000	17.372	44.631	0.833
	30	4	19.821	20.500	21.179	59.923	0.591
MEDIUM/ COMPLEX	2	4	1.978	3.500	5.022	44.178	1.750
	4	4	2.978	4.500	6.022	38.559	0.500
	10	4	4.741	6.750	8.759	34.027	0.375
COMPLEX	19	3	17.663	18.333	18.997	44.571	1.287
	30	4	22.104	25.500	28.896	53.522	0.652
LARGE/ SIMPLE	2	4	2.124	3.250	4.376	52.506	1.625
	4	4	3.470	6.250	9.030	34.832	1.500
	10	4	10.624	11.750	12.876	47.373	0.917
SIMPLE	19	2	5.058	24.000	42.942	43.809	1.361
	30	3	24.095	26.667	29.245	59.101	0.242

Numbers of taxa on Day 30 COL-substrates were compared to communities on SIMPLE communities in Part I. Assuming communities on rocks to have had sufficient time to reach an asymptote in taxa number, differences in  $S$  between substrate and rock communities may provide information regarding equilibrium times for substrate communities. I had originally hypothesized that concrete substrates which have very uniform surfaces, even in comparison to SIMPLE rocks, would support lower taxa numbers at equilibrium by providing fewer types of microhabitats. In predicting the number of taxa found on SIMPLE rocks equivalent in area to the COL-substrates (using  $S - \log A$  regressions in Part I, Table 1), taxa numbers on rock communities were similar to Day 30 COL-substrate taxa numbers (Appendix IV). If COL-substrate communities were not at an asymptote by Day 30, they were fast approaching one.

The relationship between number of taxa on Day 30 SIMPLE COL-substrates and COL-substrate area, described by simple linear regression, produced a lower slope ( $z = 0.267$ ) than encountered for communities found on SIMPLE rocks in Part I (Appendix IV). Because the substrates were all cast from the same shape of mold, SIMPLE substrates of all sizes had extremely similar topographies. There were no unique structural irregularities on larger SIMPLE substrates which could have supported additional types of taxa; structural uniformity for all SIMPLE concrete substrates would support macroinvertebrate communities with lower rates of change in taxa number with increased substrate area.

Colonization rates for most substrate types (except SMALL-SIMPLE) were high for Days 1 through 4 (Table 6). However, from Days 5 to 10, rates were low (Table 6), because the same kinds of taxa appeared each day (col-

onization rates depend upon the immigration of previously unrecorded taxa). These taxa were predominantly of three types. They were:

- 1) Large organisms able to resist strong currents.
- 2) Small organisms adapted for yielding to strong currents.
- 3) Organisms with high dispersability.

Combinations of the three types were common. Barren surfaces of Days 1 through Day 10 (with a layer of diatoms patchily covering the surface by Day 8) made current and an absence of thick algae major forces in potentially determining which taxa could exist on the substrate surface. Current resisting stone-cased caddisflies and large gastropods were common, as were current adapted Baetis and Simulium. Rapid dispersers, such as the Chironomidae, may have happened to be present at the moment of sampling, i.e. having low persistence but rapid replacement. Often, chironomids were found curled inside pores which had developed from air pockets during curing of the concrete molds. After Day 10 colonization rates rapidly increased (Days 11 to 19). Two factors may have been responsible for this increase:

- 1) On Day 14, a storm, followed by a period of high discharge, increased the number of drifting organisms and, therefore, increased the possibility of a substrate intercepting more individuals and new taxa.

- 2) At about Day 12, green algae began to form noticeable scattered patches over the surface of LARGE and MEDIUM-COMPLEX IMM- and COL-substrates. The same occurred for MEDIUM-SIMPLE IMM- and COL-substrates at around Day 14 and for SMALL-SIMPLE IMM- and COL-substrates at around Days 19 through 22. Moderate amounts of algae on the surface would have attracted and retained more immigrants by providing shelter and food, thus

lowering the probability of rapid extinction for many taxa. After Day 19, colonization rates generally declined (Table 6). By Day 19, most of the common taxa had already colonized, except (to some extent) on SMALL-SIMPLE COL-substrates. Taxa added during this final sampling interval were not common except several of the Hydracarina which, presumably, first required thick algal mats.

A definite colonization pattern had emerged. Colonization rates peaked early (Days 1 through 4) and midway (Days 10 through 19). This lack of monotonicity in colonization rate over the 30 days indicated that colonization on stream rock or substrate communities did not conform to several conditions assumed in the equilibrium theory. Because stream communities must be the result of a balance (no matter how unstable) between immigration and extinction, one or both of these processes must not be monotonic.

COL-substrate communities also exhibited a sudden increase in carrying capacity in terms of number of individuals (see growth rates, Table 7). The sudden spurt of community growth in the interval, Days 10 to 19, coincided with the establishment of thick algal patches on substrate surfaces.

Table 7. Average growth rates per sampling interval for each COL-substrate type (number of individuals / Day).

Substrate Type	Days				
	1-2	3-4	5-10	11-19	20-30
SMALL-SIMPLE	0.00	0.38	0.04	1.61	4.61
MEDIUM-SIMPLE	2.13	2.88	0.96	5.69	20.91
MEDIUM-COMPLEX	5.38	0.00	1.21	9.89	25.09
LARGE-SIMPLE	6.63	1.63	5.29	22.42	22.43

## COL-substrate Community Structure

Taxa overlap among similar COL-substrate communities (i.e. SMALL-SIMPLE, MEDIUM-SIMPLE, MEDIUM-COMPLEX, and LARGE-SIMPLE) also were similar to overlap values obtained in Part I (Table 6). This was surprising because the substrates were placed in very similar environments. If overlap is a product of environmental variability, overlap values should have been higher for stream communities on rocks where variability was greatest. Taxa composition and turnover of benthic communities may be affected by other factors independent of physical variability.

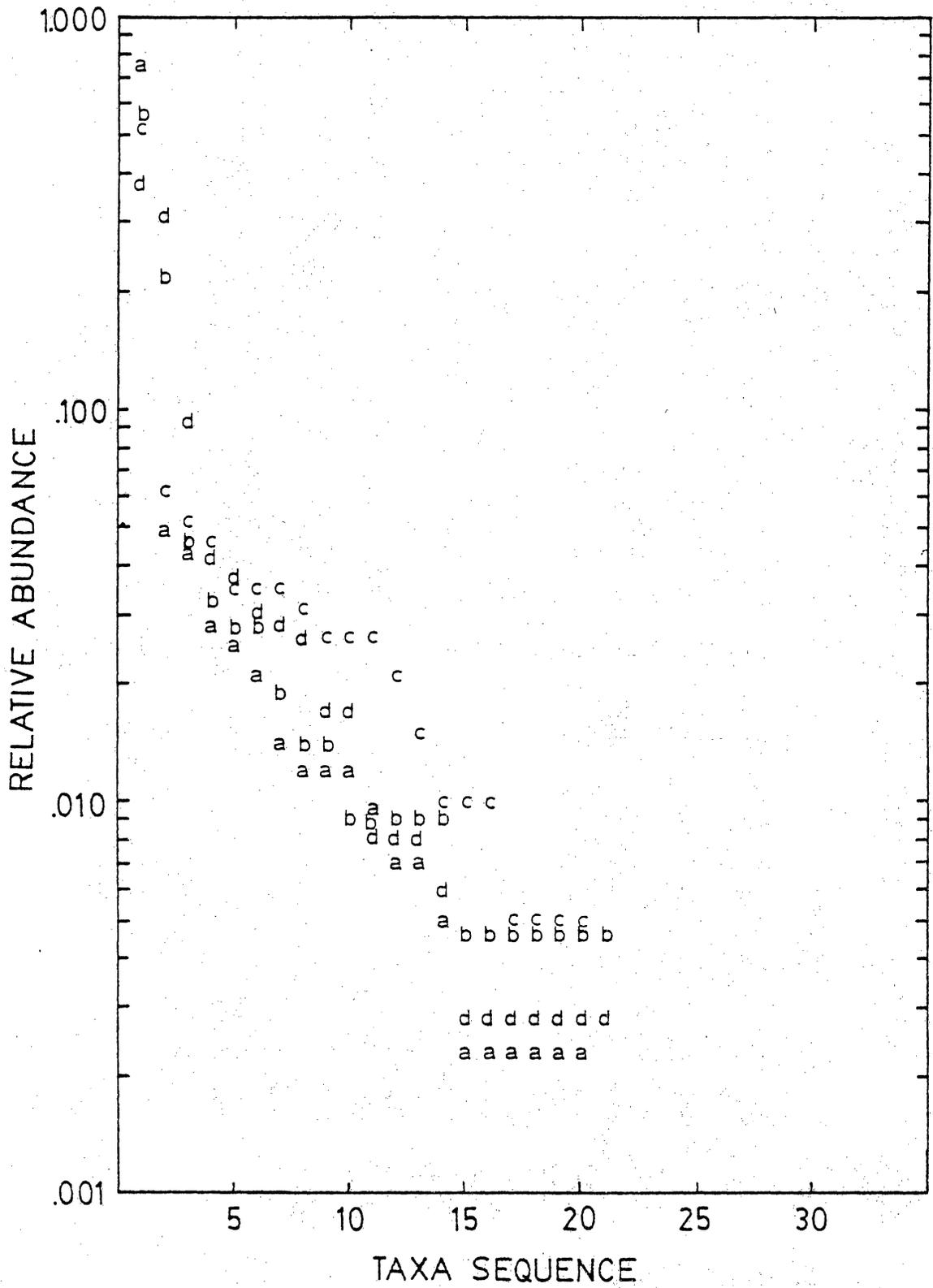
Dominance-diversity curves for Day 30 COL-substrates were different from those of Part I (e.g. Figures 7 and 8). Greater dominance was found in LARGE COL-substrate communities, MEDIUM-SIMPLE and MEDIUM-COMPLEX communities than in communities on LARGE or MEDIUM rock communities. LARGE and MEDIUM substrates supported thick algal mats, usually thicker than on nearby rocks (a personal observation for all times of the year). Thicker mats could select for a greater dominance by the Chironomidae and Hydracarina at the expense of other taxa, especially the Ephemeroptera, Trichoptera, and Simulium. Densities of these taxa groups were considerably lower on the COL-substrates than in the fall experiment (Part I). Perhaps they were not as common in the late winter (i.e. when Part II was performed) or more common, but less active. The former seems doubtful, because all three taxa groups were common on IMM-substrates (see later sections). COL-substrate communities also had fewer taxa in the intermediate relative abundance range of 0.1 to 0.01 than communities on rocks, again demonstrating greater dominance on substrate communities.

SMALL-SIMPLE COL-substrate communities had dominance-diversity

Figure 7. Dominance - diversity relationships for SMALL-SIMPLE COL-substrate communities on Day 30 (each lettered symbol denotes a community).



Figure 8. Dominance - diversity relationships for MEDIUM-SIMPLE COL-substrate communities on Day 30 (each lettered symbol denotes a community).



curves similar to communities on SMALL rocks (Figure 7) though, even here, dominance was greater than expected. Greater similarity between the two SMALL collections (COL-substrate and rock) could have resulted from the observation that SMALL-SIMPLE COL-substrate communities never supported thick algal mats characteristic of larger COL-substrates.

Densities of most taxa (number of individuals /  $\text{cm}^2$ ) generally decreased with increasing size of the substrate (Table 8). In comparing SIMPLE and COMPLEX COL-substrate communities (Day 30), 64% of the taxa occurred in greater densities on COMPLEX COL-substrate communities. This was approximately 6-15% higher than the same percentage calculated between SIMPLE and COMPLEX communities in Part I. Again, the assumption that larger and more complex islands have lower extinction rates because of a greater population size for each taxon does not strictly apply to communities on stream rocks or substrates (see Simberloff, 1976a, p.629). If individuals to a given taxon can be rapidly replaced upon extinction (i.e. by high invasion), population size is not necessarily an indication of a taxon's extincibility in a given community found on stream rocks or substrates.

Table 8. Taxa list for colonization and immigration segments of Part II. Included, are the average taxa population densities (number of individuals / cm<sup>2</sup> \* 100) found on Day 30 COL-substrate communities.

TAXA	SMALL/ SIMPLE	MEDIUM/ SIMPLE	MEDIUM/ COMPLEX	LARGE/ SIMPLE
Ephemeroptera				
Baetidae				
<u>Baetis</u>	...	0.55	0.36	0.13
<u>Ephemerella</u>	0.81	0.36	0.46	0.07
<u>Isonychia</u>	...	0.09	0.27	0.03
Heptageniidae				
<u>Heptagenia</u>	...	...	0.09	0.20
<u>Epeorus</u>	...	0.27	0.27	0.10
<u>Stenonema</u>	...	0.18	0.55	0.30
Trichoptera				
Hydropsyche				
<u>Hydropsyche</u>	...	0.63	0.36	0.13
Hydroptilidae				
Hydroptilid spp.	0.81	0.82	2.37	0.59
Philopotamidae				
<u>Chimarra</u>	...	...	0.36	...
<u>Wormaldia</u>	...	...	0.09	0.03
Rhyacophilidae				
<u>Rhyacophila</u>	...	...	...	...
<u>Glossosoma</u>	1.16	0.91	2.83	1.81
Limnephilidae				
<u>Neophylax</u>	...	0.18	2.37	0.10
Helicopsychidae				
<u>Helicopsyche</u>	...	...	...	0.03
Plecoptera				
Nemouridae				
<u>Taeniopteryx</u>	...	...	...	...
<u>Brachyptera</u>	...	...	...	...

Table 8 (cont.). Taxa list for colonization and immigration segments of Part II. Included, are the average taxa population densities (number of individuals / cm<sup>2</sup> \* 100) found on Day 30 COL-substrate communities.

TAXA	SMALL/ SIMPLE	MEDIUM/ SIMPLE	MEDIUM/ COMPLEX	LARGE/ SIMPLE
Perlidae				
<u>Neoperla</u>	...	...	0.18	...
Coleoptera				
Elmidae				
<u>Optioservus</u>	...	...	0.09	...
<u>Stenelmis</u>	...	...	...	0.03
Psephenidae				
<u>Psephertus</u>	...	...	...	...
Diptera				
Blephariceridae				
<u>Blepharicera</u>	...	...	...	...
Chironomidae				
Chironomid #3	...	...	...	...
Chironomid #7	7.26	13.59	8.49	1.45
Chironomid #8	4.03	3.01	0.57	0.49
Chironomid #9	127.42	59.58	96.90	33.60
Chironomid #10	...	...	...	...
Chironomid #12	4.03	1.55	0.73	0.49
Chironomid #14	3.23	0.27	0.73	0.13
Chironomid #15	...	...	...	...
Chironomid #18	7.26	2.92	4.65	0.79
Chironomid #19	1.61	3.01	2.10	0.13
Chironomid #20	...	...	0.18	...
Chironomid #21	....	....	....	...
Chironomid #22	4.03	3.56	6.84	0.30
Chironomid #23	...	...	...	0.03

Table 8 (cont.). Taxa list for colonization and immigration segments of Part II. Included, are the average taxa densities (number of individuals / cm<sup>2</sup> \* 100) found on Day 30 COL-substrate communities.

TAXA	SMALL/ SIMPLE	MEDIUM/ SIMPLE	MEDIUM/ COMPLEX	LARGE/ SIMPLE
Chironomid #24	...	...	...	...
Chironomid #25	...	...	...	0.03
Rhagionidae				
<u>Atherix</u>	5.65	1.55	1.28	0.57
Simulidae				
<u>Simulium</u>	...	0.09	1.73	0.30
<u>Prosimulium</u>	...	...	0.18	...
Tipulidae				
<u>Antocha</u>	...	0.09	0.55	0.03
Oligochaetae	28.23	6.20	9.49	2.44
Amiphipoda	...	0.09	...	...
Turbellaria	...	...	...	0.03
Acari				
Hydracarina				
Hydracarina #1	0.81	...	...	...
Hydracarina #2	3.23	...	0.55	...
Hydracarina #3	...	...	...	0.13
Hydracarina #4	...	0.27	0.27	0.13
Hydracarina #6	...	...	...	...
Hydracarina #7	...	...	...	...
Hydracarina #8	0.81	0.46	1.09	0.59
Hydracarina #9	...	0.09	0.91	...
Hydracarina #10	1.61	0.91	0.36	0.43
Hydracarina #11	0.81	...	...	0.30
Hydracarina #15	...	...	...	...
Hydracarina #16	...	...	...	...
Hydracarina #19	4.84	3.74	3.92	2.37

Table 8 (cont.). Taxa list for colonization and immigration segments of Part II. Included, are the average taxa densities (numbers of individuals /  $\text{cm}^2 * 100$ ) found on Day 30 COL-substrate communities.

TAXA	SMALL/ SIMPLE	MEDIUM/ SIMPLE	MEDIUM/ COMPLEX	LARGE/ SIMPLE
Hydracarina #20	...	0.27	0.09	...
Hydracarina #21	...	0.09	...	0.03
Mollusca				
Pleuroceridae				
<u>Goniobasis</u>	3.23	1.00	1.55	0.69
<u>Nitocris</u>	2.42	1.92	1.82	1.25
Collembola	...	...	...	...

### Immigration

With an absence of a distance effect, it was hypothesized that substrate size could determine the magnitude of immigration. Larger substrates, by presenting a bigger target, should intercept more drifting individuals and increase the possibility of intercepting more taxa. By Day 36, larger IMM-substrates accumulated more taxa than smaller IMM-substrates (Figures 9 and 10). In calculating a linear regression with Log A as the independent variable and total number of taxa by Day 36 as the dependent variable, the slope was significantly greater than zero and positive for SIMPLE and COMPLEX IMM-substrates (Figure 11). Evidence of higher cumulative immigration with increasing size was, however, equivocal. Differences in cumulative taxa numbers by Day 36 among MEDIUM-SIMPLE, MEDIUM-COMPLEX, NEW MEDIUM-COMPLEX, INTERMEDIATE-COMPLEX, LARGE-SIMPLE, AND LARGE-COMPLEX IMM-substrates were small as were the differences between SMALL-SIMPLE, INTERMEDIATE-SIMPLE, NEW MEDIUM-SIMPLE IMM-substrates (see Figures 9, 10, and 11). If the experiment could have continued another 20 days or so, it would be impossible to predict which IMM-substrates would have accumulated the highest taxa numbers. Smaller IMM-substrates may receive as many taxa almost as fast as larger substrates (e.g. as shown among COMPLEX IMM-substrates, the INTERMEDIATE-COMPLEX IMM-substrate was accumulating taxa almost as fast as larger COMPLEX IMM-substrates, Figure 9). An important question here, then, is how long does it take for smaller substrate communities to reach an asymptote in taxa number. If the time is short, with smaller substrates accumulating as many taxa shortly after larger substrates reach an asymptote, the importance

Figure 9. Cumulative immigration curves for COMPLEX IMM-substrates.

(i)...INTERMEDIATE

(s)...NEW MEDIUM

(c)...MEDIUM

(l)...LARGE

(n)...NATL rock

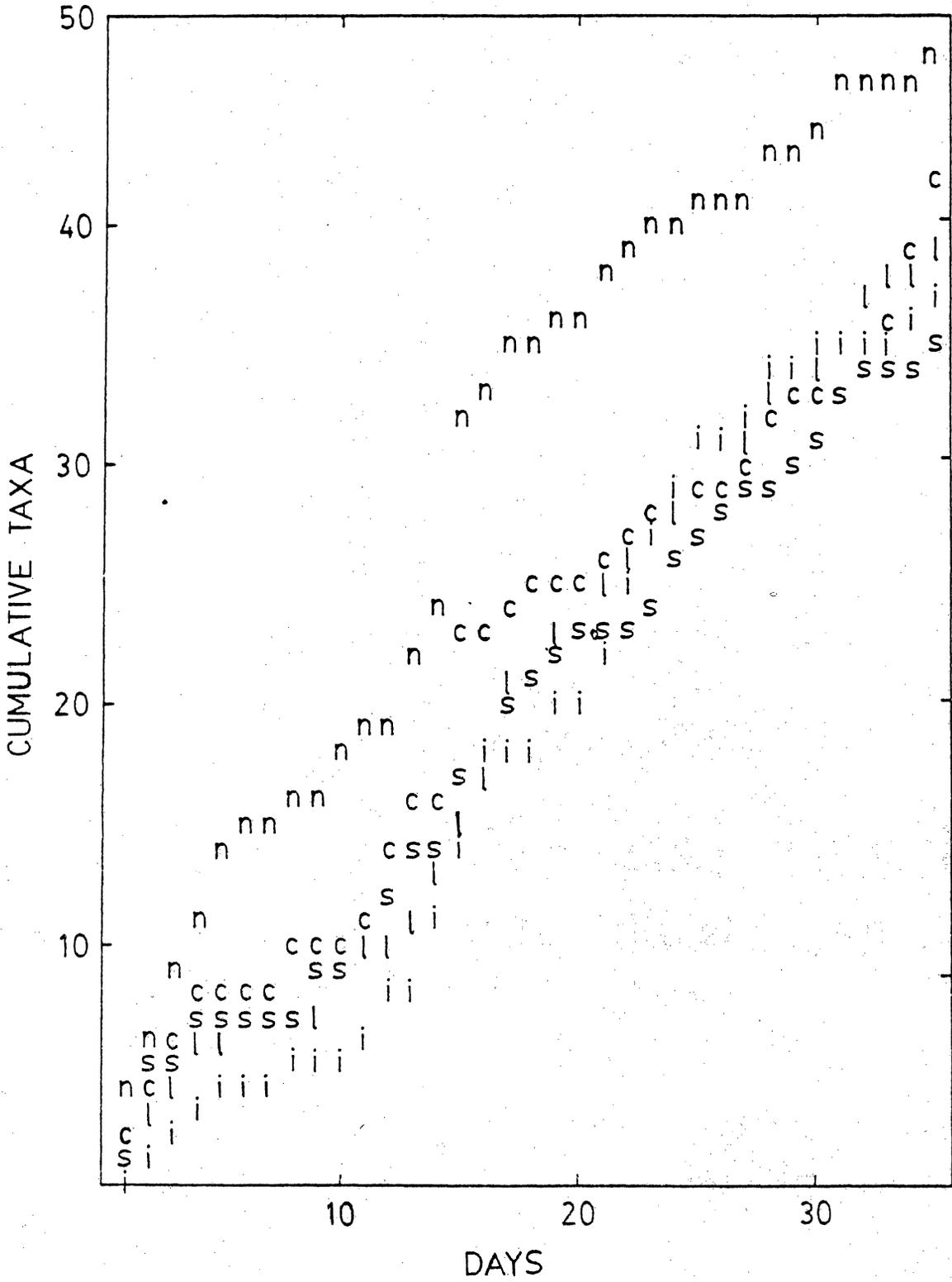


Figure 10. Cumulative immigration curves for SIMPLE IMM-substrates.

(n)...SMALL #3

(v)...SMALL #4

(i)...INTERMEDIATE

(s)...NEW MEDIUM

(o)...MEDIUM

(l)...LARGE

(?)...missed sampling days

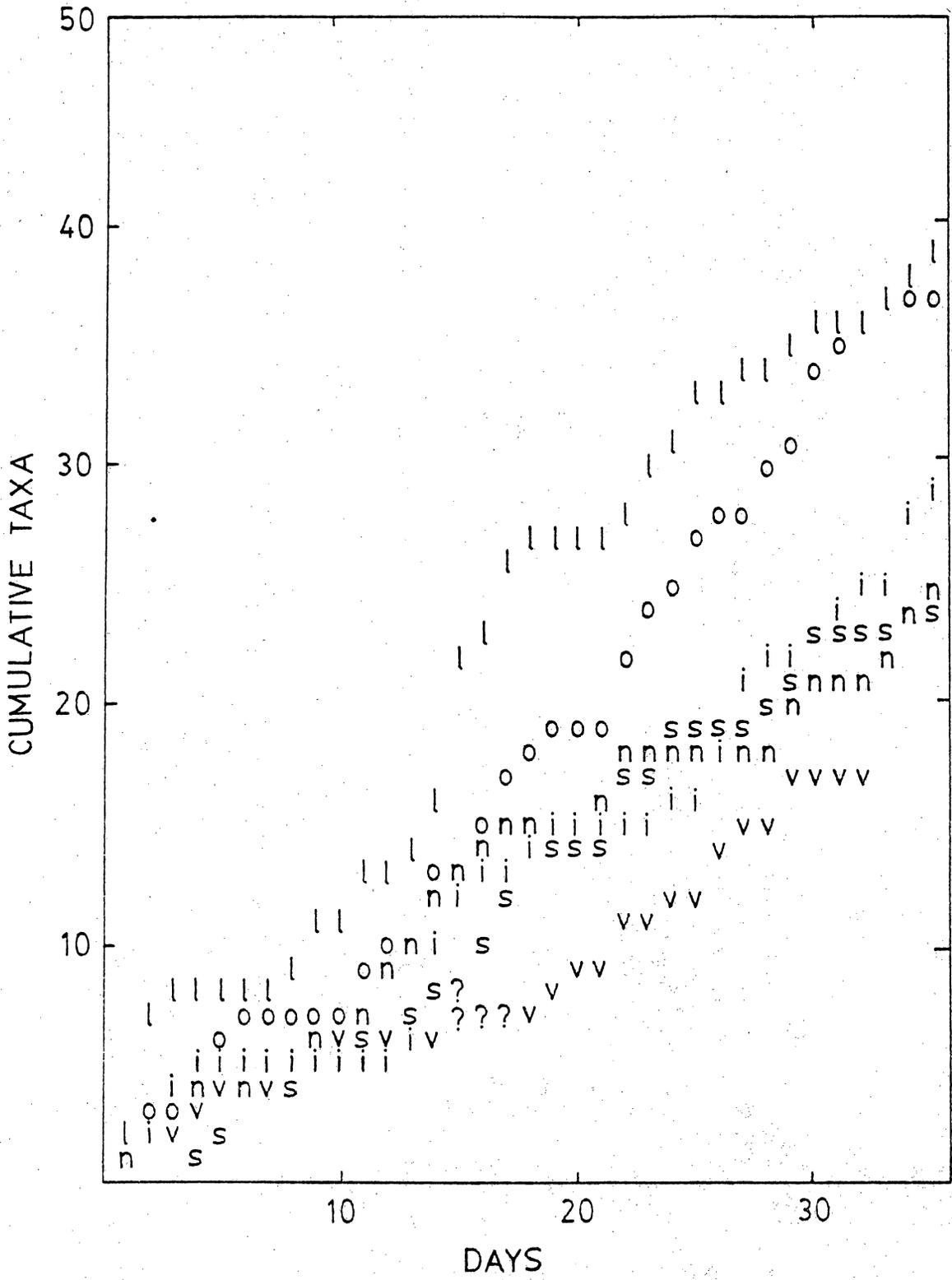


Figure 11. Day 30 cumulative immigration plotted as a function of IMM-substrate area. The taxa-area curve for Day 30 SIMPLE COL-substrate communities is labeled "COLONIZATION" (see Table 6 for supporting statistics).

(s)...SIMPLE IMM-substrate

(c)...COMPLEX IMM-substrate

(nc)..NEW MEDIUM-COMPLEX IMM-substrate

(ns)..NEW MEDIUM-SIMPLE IMM-substrate

(nc)..NATL-COMPLEX rock



of immigration rates in determining taxa number at equilibrium on COL-substrate or rock communities may not be as important as other processes such as extinction and invasion. Higher extinction rates for communities on smaller substrates (as predicted by MacArthur and Wilson, 1967, for islands in general) would account for fewer taxa on COL-substrate or rock communities. Another factor may be equally as important. The effect of extinction at lowering taxa numbers would be offset if communities underwent high rates of invasion and replacement. Both of these processes are examined in other sections.

Cumulative immigration curves were approximately linear (a linear regression could not be performed because the data were dependent)(Figures 9 and 10). These two features were prominent:

- 1) During Days 5 through 10, immigration was constantly low, creating a small plateau in the curves. A layer of slushy anchor ice on Day 7 (melting by noon) along with the low diversity of taxa adapted for surviving (even temporarily) on barren surfaces, contributed to this low rate.

- 2) A large increase in new taxa during Days 15 and 16, coinciding with a period of high discharge, dramatically increased immigration rates. This sudden influx of new taxa had an additional effect. Immigration rates for the following days (Days 19 through 30) were forced lower by having an usually high number of new taxa appear earlier than expected.

Due to their erratic behavior, daily immigration rates were averaged over the same time intervals used in the colonization segment of the experiment. A general shape emerged (Figure 12). Immigration curves peaked

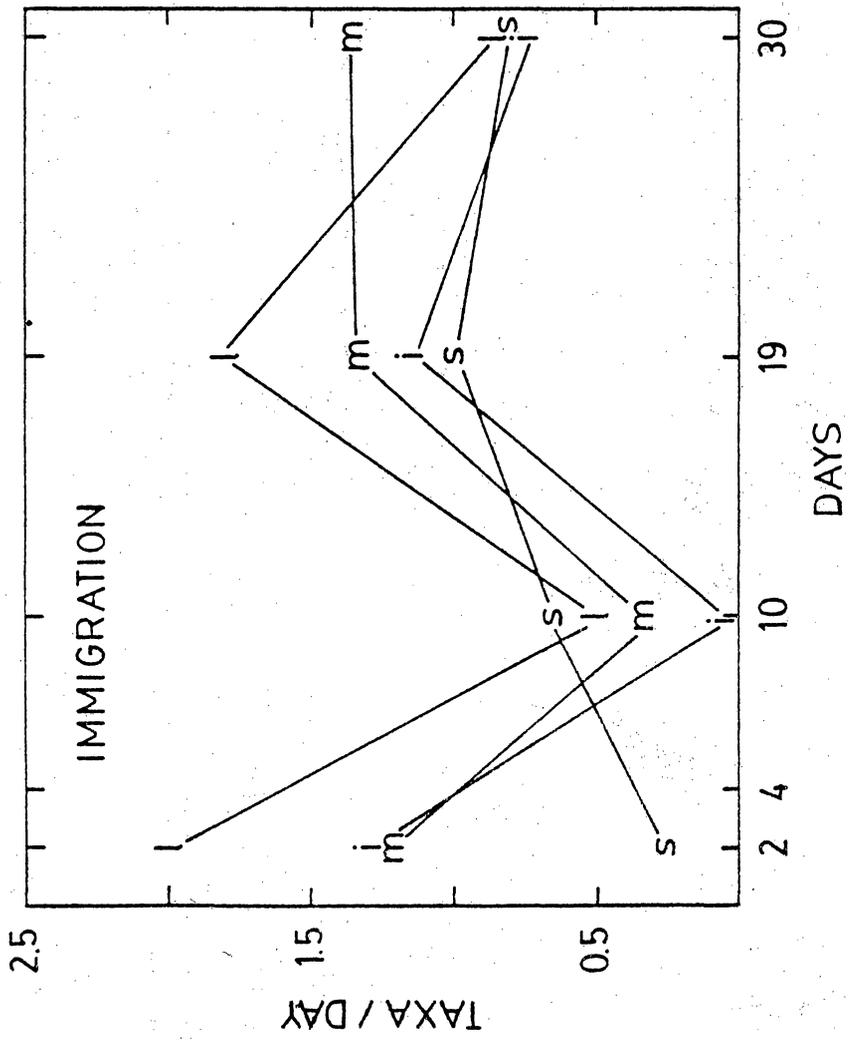
Figure 12. Average SIMPLE IMM-substrate immigration rates for each sampling period (number of taxa / Day).

(l)...LARGE IMM-substrate

(m)...MEDIUM IMM-substrate

(i)...INTERMEDIATE IMM-substrate

(s)...SMALL IMM-substrate



early (Days 1 to 4) and midway (Days 14 to 17) through the 36 day experiment, closely following the trend in colonization rates (compare Table 6 and Appendix V).

The MacArthur and Wilson (1967) equilibrium model assumes a monotonically decreasing immigration rate. Immigration rate curves were not monotonic for stream benthic communities. This does not, however, necessarily detract from the equilibrium model because the substrates did not remain ecologically constant through time (a necessary condition in the model); the gradual accumulation of algae, from initially barren surfaces to densely covered surfaces by Day 30, certainly altered the environment of concrete substrates through time.

Cumulative taxa number by Day 36 was as high on the NEW MEDIUM-COMPLEX IMM-substrate as on the undisturbed MEDIUM-COMPLEX IMM-substrate (Figure 9). The NEW MEDIUM-SIMPLE IMM-substrate, though, had many fewer taxa than the MEDIUM-SIMPLE IMM-substrate: indicating that algal colonization, especially for COMPLEX IMM-substrates, was not of paramount importance in determining immigration rates. Some algal colonization did occur on NEW IMM-substrates; both developed a pale green hue even with the daily scrubbing. Algae that were colonizing small crevices and pores could have provided a favorable habitat for certain immigrating taxa that might not have otherwise survived. In the later 1/3 of the experiment (Days 20 through 30) relatively large numbers of Chironomidae were found on the NEW MEDIUM IMM-substrates indicating that, in some manner, the NEW IMM-substrates had increased their carrying capacity. Increased carrying capacity could have been the result of limited algal colonization (creating more microhabitats).

The design for determining an algal effect on immigration had its shortcomings. It would have been better to have introduced unused substrates (substrates without any chance of algal colonization) on each sampling day rather than using the same substrate (though scrubbed).

The eventual fate of the immigration rate curves deserves an explanation. The manner in which immigration rate was determined, i.e. the appearance of new taxa with time, would lead us to predict that, eventually, the immigration rate would be very close to zero. As a cumulative immigration curve accounted for almost all taxa that could be intercepted from the immigration pool, further additions would only come from the appearances of either infrequent taxa or new taxa just emerging from eggs. However, immigration rates were considered independently of the colonization processes (i.e. these immigration rates are estimates of the slope of cumulative immigration curves). As turnover on an island (or rock) community occurs, a former colonist, now extinct from a given rock or substrate, again qualifies as an immigrant upon its re-appearance on the same rock or substrate. If turnover is high, the same taxon may qualify as an immigrant many times during the life span of a given community. This will keep immigration rates high, even after equilibrium.

## Extinction

Higher extinction rates were not a function of decreasing substrate area. The slope of the relationship between cumulative numbers of immigrants on Day 30 IMM-substrates and IMM-substrate area was parallel to the slope of the relationship between numbers of taxa on Day 30 COL-substrates and COL-substrate area (Figure 11). The colonization-area curve, in comparison to the cumulative immigration-area curve, was displaced downward by approximately 10 taxa for all SIMPLE substrate areas. Though extinction rate was constant with area, extinction accounted for a greater percentage of the immigrating taxa on smaller substrates (i.e. the ratio, number of taxa on Day 30 COL-substrates / cumulative number of taxa on IMM-substrates) by Day 30, was decreasing with increasing substrate area.

MEDIUM-COMPLEX substrate communities had higher extinction rates early, but had lower rates during the last 15 days of colonization in comparison to MEDIUM-SIMPLE substrate communities (Appendix VI). An averaging of extinction rate over the entire 30 days indicated that communities on COMPLEX substrates had slightly higher overall extinction rates.

Extinction rates fluctuated throughout the 30 days of colonization, with no clear trend (variation in rate with time) among substrate types (Appendix VI). All the above conclusions and observed variability in rate (and for immigration estimates as well) are based on the first 30 days of colonization. Because these communities did not appear to be at an equilibrium by Day 30, the relationships between area and various processes (e.g. immigration, extinction, and invasion) could change after equil-

ibrium. Also, extinction rates do not account for taxa turnover (because no available technique exists for measuring turnover on a stream rock). Therefore, turnover has been implied to be constant with substrate area; I have no unequivocal evidence for or against this implication.

### Invasion and Replacement

Clearly, invasion rates (Table 9) were higher for larger substrates (separate linear regressions, with area as the independent variable and Day 30 cumulative invasion as the dependent variable on SIMPLE and COMPLEX IMM-substrates, produced slopes that were greater than zero and positive). For example, in the interval, Days 20 to 30, the LARGE-COMPLEX IMM-substrate was receiving over twice as many individuals, daily, than the INTERMEDIATE-COMPLEX IMM-substrate. The effect of area on invasion rates for SIMPLE IMM-substrates was similar (Figure 13), though not as pronounced.

A characteristic dip in invasion rate was consistent during Days 5 to 10 for all IMM-substrates except SMALL-SIMPLE IMM-substrates (Table 9). Colonization and immigration rates also exhibited this dip. While decreases in immigration rate could be explained as an absence in arrival of new taxa due to harsh substrate conditions, there was no intuitive reason to expect decreasing invasion rates if conditions remained the same as in Days 1 through 4. As noted earlier, a slushy anchor ice which formed over the night of Day 6 could have, due to a drop in temperature, lowered drift densities (Waters, 1972) and, consequently, lowered invasion.

New SIMPLE and COMPLEX IMM-substrates received approximately 3 times fewer individuals than their undisturbed counterparts (Table 9). This divergence in invasion rate (between disturbed and undisturbed substrates) did not occur until Days 11 to 19; just when algae were becoming established on IMM-substrates. The importance of algae, which does not always affect certain rates (e.g. immigration rates for COMPLEX IMM-

Table 9. Average invasion rates for each sampling interval for all IMM-substrates expressed as the number of individuals per Day.

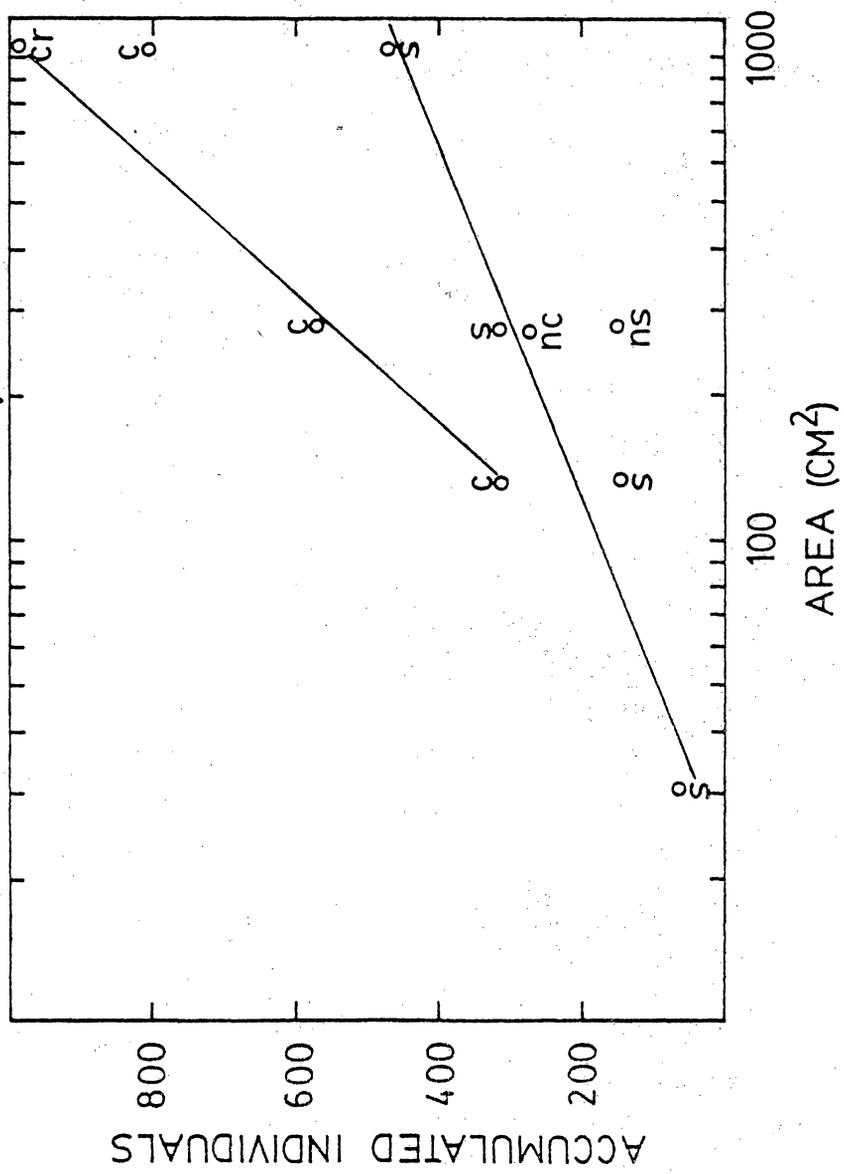
Substrate Type	Days				
	1-2	3-4	5-10	11-19	20-30
SMALL-SIMPLE #3	0.00	0.50	0.67	2.11	4.45
SMALL-SIMPLE #4	1.50	0.50	0.83	1.56	5.91
INTERMEDIATE-SIMPLE	3.00	3.00	1.50	5.33	7.45
INTERMEDIATE-COMPLEX	1.50	3.50	1.50	8.75	21.55
NEW MEDIUM-SIMPLE	4.50	6.50	2.17	6.89	5.64
MEDIUM-SIMPLE	4.50	3.00	3.33	11.22	18.45
NEW MEDIUM-COMPLEX	10.00	8.50	5.17	8.78	13.55
MEDIUM-COMPLEX	9.00	6.00	4.83	16.67	37.36
LARGE-SIMPLE	12.00	9.50	6.67	14.56	26.91
LARGE-COMPLEX	13.00	11.00	6.17	21.22	56.45
NATL-COMPLEX	31.00	19.50	14.50	36.44	58.70

Average replacement rates for each sampling interval for all IMM-substrates expressed as the number of taxa per Day.

Substrate Type	Days				
	1-2	3-4	5-10	11-19	20-30
SMALL-SIMPLE #3	0.00	0.50	0.67	1.56	2.91
SMALL-SIMPLE #4	1.50	0.50	0.83	1.22	3.36
INTERMEDIATE-SIMPLE	1.00	3.00	1.33	3.22	4.55
INTERMEDIATE-COMPLEX	0.50	1.50	1.33	5.22	7.82
NEW MEDIUM-SIMPLE	1.00	2.50	1.50	4.44	3.82
MEDIUM-SIMPLE	2.00	2.00	1.67	6.56	7.09
NEW MEDIUM-COMPLEX	3.00	3.50	3.33	5.44	6.36
MEDIUM-COMPLEX	2.50	4.00	3.17	8.89	9.18
LARGE-SIMPLE	4.00	4.50	3.20	6.89	8.81
LARGE-COMPLEX	2.50	4.50	2.83	8.22	9.82
NATL-COMPLEX	4.00	7.00	6.67	12.44	11.80

Figure 13. Day 30 cumulative invasion plotted as a function of substrate area.

- (s)...SIMPLE IMM-substrate
- (c)...COMPLEX IMM-substrate
- (nc)..NEW MEDIUM-COMPLEX IMM-substrate
- (ns)..NEW MEDIUM-SIMPLE IMM-substrate
- (cr)..NATL-COMPLEX rock



substrates), does greatly affect invasion rates.

Invasion rates exhibited a greater increasing trend with area than did immigration rates; IMM-substrate types exhibited smaller cumulative differences in immigration but larger differences in invasion. With high extinction, the rate at which individuals arrive and replace lost individuals will be of major importance in maintaining high stream community taxa number. Replacement rates closely followed invasion rates (Table 9); a Spearman Rank Correlation Coefficient between Day 30 invasion and replacement rates was 0.991. High average replacement rate during the last sampling interval sometimes, in a single day, accounted for 1/3 or more of the total number of taxa found on a Day 30 COL-substrate community. Therefore, immigration rates, though informative, are not complete in describing the colonization process. A rescue effect (described by Brown and Kodric-Brown, 1977) could apply here with taxa populations being maintained by high invasion that otherwise would rapidly go extinct. Low invasion and replacement rates on SMALL-SIMPLE substrates (Tables 9 and 10) coupled with extinction rates similar to larger substrate communities could result in low taxa numbers (as found on Day 30 SMALL-SIMPLE COL-substrate communities).

### Comparison of COL-substrate Communities to the Immigration Pool

The purpose of this section is to compare relative abundance structures of COL-substrate communities (Day 30) and their respective immigration pools for similarities in relative abundance among major taxa (Table 10). If COL-substrate communities are formed by random selection of individuals from the immigration pool, relative abundances of COL-substrate communities should approximate the relative abundance structure of their respective immigration pool. This statement, however, assumes equal probabilities of extinction for all taxa. If certain taxa are more prone to extinction and if the most common immigrating taxa (having higher relative abundances) have low extinctability wherever they settle, the space vacated by extinction prone taxa will have a greater chance of being occupied by more common taxa. Eventually, communities will be dominated by less extinction prone taxa, disproportionate to their relative abundance in the immigration pool.

Relative abundances of the Chironomidae in the later 2 intervals were always overrepresented in COL-substrate communities in comparison to their immigration pools (Table 10). This suggests that the Chironomidae, for the later half of the experiment, had low extinctabilities. Actually, relative abundances of the Chironomidae within the immigration pools were probably greater than indicated because of sampling technique. A mild jet of water could not remove all the smaller Chironomidae, Hydracarina, and possibly very small Baetis, from the algal mat. Gentle rinsing was necessary so as not to disturb algal colonization; COL- and IMM-substrates had to be kept as similar as possible over the 30 days.

Table 10. Relative abundances within 7 major groups of taxa for all sampling intervals found on COL-substrate communities and IMM-substrate immigration pools.

TAXA	SUBSTRATE TYPE	SMALL-SIMPLE DAYS			
		1-4	5-10	11-19	20-30
Chironomidae	COL	...	0.250	0.803	0.764
	IMM	0.500	0.500	0.632	0.688
Hydracarina	COL	...	...	0.049	0.058
	IMM	...	...	0.053	0.125
Ephemeroptera	COL	...	...	0.016	0.004
	IMM	...	0.250	...	0.063
Trichoptera	COL	...	0.250	0.098	0.012
	IMM	...	...	0.053	0.021
Mollusca	COL	...	...	0.016	0.027
	IMM	...	...	0.105	0.042
Oligochaetae	COL	...	...	...	0.136
	IMM	...	...	0.053	...
Simuliidae	COL	...	0.500	0.016	...
	IMM	0.500	0.250	0.105	0.063

Table 10 (cont.). Relative abundances within 7 major groups of taxa on all sampling intervals found on COL-substrate communities and IMM-substrate immigration pools.

TAXA	SUBSTRATE TYPE	MEDIUM-SIMPLE			
		1-4	5-10	11-19	20-30
Chironomidae	COL	0.150	0.333	0.558	0.820
	IMM	0.071	0.050	0.394	0.605
	NEW IMM	0.048	0.083	0.344	0.565
Hydracarina	COL	...	...	0.025	0.055
	IMM	...	...	0.030	0.118
	NEW IMM	...	0.083	0.016	0.044
Ephemeroptera	COL	0.100	0.032	0.041	0.014
	IMM	...	0.050	0.020	0.041
	NEW IMM	...	...	0.082	0.109
Trichoptera	COL	0.125	0.095	0.107	0.025
	IMM	...	...	0.071	0.041
	NEW IMM	...	...	0.033	0.022
Mollusca	COL	0.125	0.079	0.142	0.027
	IMM	0.071	...	0.232	0.046
	NEW IMM	...	...	0.049	...
Oligochaetae	COL	...	...	0.015	0.058
	IMM	...	...	...	0.014
	NEW IMM	...	...	...	...
Simuliidae	COL	0.500	0.460	0.112	0.001
	IMM	0.857	0.900	0.253	0.136
	NEW IMM	0.952	0.833	0.475	0.261

Table 10 (cont.). Relative abundances within 7 major groups of taxa on all sampling intervals found on COL-substrate communities and IMM-substrate immigration pools.

TAXA	SUBSTRATE TYPE	MEDIUM-COMPLEX			
		1-4	5-10	11-19	20-30
Chironomidae	COL	0.119	0.443	0.738	0.757
	IMM	0.188	0.179	0.514	0.721
	NEW IMM	0.111	0.133	0.372	0.469
Hydracarina	COL	...	0.014	0.024	0.051
	IMM	...	...	0.027	0.165
	NEW IMM	...	0.033	0.039	0.109
Ephemeroptera	COL	0.095	0.100	0.037	0.015
	IMM	...	0.250	0.144	0.059
	NEW IMM	0.056	0.233	0.077	0.061
Trichoptera	COL	0.119	0.057	0.040	0.061
	IMM	...	0.036	0.021	0.018
	NEW IMM	...	...	0.103	...
Mollusca	COL	0.024	...	0.049	0.037
	IMM	0.063	0.036	0.048	0.003
	NEW IMM	0.028	...	0.167	0.020
Oligochaetae	COL	0.024	...	0.043	0.067
	IMM	...	...	...	...
	NEW IMM	...	...	...	0.041
Simuliidae	COL	0.619	0.386	0.070	0.013
	IMM	0.750	0.500	0.247	0.034
	NEW IMM	0.801	0.600	0.244	0.293

Table 10 (cont.). Relative abundances within 7 major groups of taxa on all sampling intervals found on COL-substrate communities and IMM-substrate immigration pools.

TAXA	SUBSTRATE TYPE	LARGE-SIMPLE			
		1-4	5-10	DAYS 11-19	20-30
Chironomidae	COL	0.095	0.553	0.829	0.759
	IMM	0.116	0.128	0.277	0.542
Hydracarina	COL	...	0.005	0.018	0.081
	IMM	...	0.026	0.050	0.219
Ephemeroptera	COL	0.095	0.047	0.026	0.017
	IMM	0.116	0.103	0.126	0.040
Trichoptera	COL	0.079	0.026	0.041	0.049
	IMM	0.047	...	0.025	0.010
Mollusca	COL	0.048	0.121	0.053	0.039
	IMM	...	...	0.135	0.024
Oligochaetae	COL	...	...	0.008	0.049
	IMM	...	...	0.008	0.010
Simulidae	COL	0.683	0.247	0.024	0.006
	IMM	0.721	0.744	0.378	0.155

Therefore, there was a greater relative abundance of chironomids on IMM-substrate immigration pools, though not by more than a 10% increase (as found in pilot experiments). Interestingly, the relative abundance of the Chironomidae in the NEW MEDIUM-SIMPLE IMM-substrate immigration pool was very similar to that in the MEDIUM-SIMPLE IMM-substrate immigration pool. I had originally thought that chironomid relative abundance would be less on the NEW MEDIUM-SIMPLE IMM-substrate because the absence of thick algae would make the substrate surface less suitable to immigrating Chironomidae. Oligochaetae were overrepresented on COL-substrate communities in comparison to their immigration pool.

In contrast, the relative abundance of Simuliidae was extremely low on COL-substrate communities in comparison to the immigration pool. Thick algal mats which would interfere with their feeding, could make the Simuliidae more extinction prone. An indication that algae may be an important factor was the observed high relative abundance of Simuliidae during the last two intervals in NEW MEDIUM-SIMPLE and -COMPLEX IMM-substrate immigration pools (see Table 10). Ephemeroptera and Hydracarina also were usually underrepresented on COL-substrate communities. Mollusca and Trichoptera were extremely variable, making it difficult to generalize.

Relative abundances of all taxa within a given immigration pool changed with time. Because there was little reason to suspect that the drift would have substantially changed (compositionally) over the 36 days, the IMM-substrates, themselves, must have changed. The gradual colonization of algae provided an environmental change through time;

selecting for different taxa with increasing algae. The colonization of algae on IMM-substrates occurred in the same manner as on COL-substrates (see colonization section). Simuliidae, Ephemeroptera, and Trichoptera (to some extent) decreased in relative abundance with time while the Chironomidae, Hydracarina, and Oligochaetae increased in relative abundance.

In summary, relative abundance structures of COL-substrate communities did not reflect the relative abundance structure of the immigration pool, showing that differential extinction among major taxa groups did occur.

## PART II

### SUMMARY

Larger and more complex substrates intercepted more individuals (invasion rate), and, if the size difference between contrasted substrates was great, also intercepted more taxa. The taxa number - area curve for Day 30 COL-substrates closely paralleled their cumulative immigration - area curve (Figure 11) indicating that extinction was independent of area. COMPLEX substrates had higher invasion, colonization, and immigration rates than SIMPLE substrates: though differences (between SIMPLE and COMPLEX substrates of the same area) in immigration and colonization were small. Taxa numbers on COL-substrate communities could be characterized as a result of high turnover; a balance between high invasion (and replacement) and high extinction. Taxa overlap between similar communities remained low, even after a reduction in environmental variability.

The technique of sampling substrates over discrete time intervals and the inability to "track" individuals through time generated an interesting question. How does high extinction occur? Does a one day old colonist have a less, greater, or equal chance of extinction compared to an immigrant belonging to the same taxon which is only 2 minutes old or another individual of the same taxon that is a veteran of 15 days? The influence of territoriality and other interactions can only be guessed. Perhaps most extinction occurs among the daily immigrants (especially as available space becomes limiting when a community approaches equilibrium), with few established colonists (2 days residence or longer)

going extinct. Turnover of individuals, therefore, would be high for newly arriving colonists and low for established colonists. The ratio, initial colonist turnover / established colonist turnover, would increase over the 30 days of this experiment because organisms down in the algal mats should be less exposed to harsh environmental factors while a newly arriving organism must try to gain an initial foothold while being fully exposed to environmental stress and exposure to predators. An individual landing on a rock that supports an equilibrium community may find available space to be extremely limiting, thereby forcing emmigration. On barren surfaces (Days 1 through 10) immigrating as well as established individuals are exposed to similar environments, equalizing the chance of extinction. Until individuals can be observed continually, estimates of turnover will remain a conjecture.

PART III  
A Simulation of Benthic Community Colonization  
on  
Stream Substrates

INTRODUCTION

Colonization is a well documented "endpoint" but a little understood process. Intuitively, the number of species on an island (the "endpoint") must be a balance (no matter how tenuous) between immigration and emmigration. In Part II, colonization and immigration were determined independently; their difference provided a conservative estimate of emmigration. As colonization continued through the 30 days, each substrate "island" was continually exposed, daily, to large numbers of invading organisms. How important an influence is the qualitative and quantitative composition of the invasion pool on the formation of stream macroinvertebrate communities? Are communities a collection of randomly selected individuals from the invasion pool or are communities, during colonization, proceeding in an orderly fashion towards a deterministic equilibrium, shaped by interactions involving physical and biotic dimensions of the developing community?

Part II provided evidence that neither option (above) could be entirely true for the first 30 days of colonization. The slope of the relationship between accumulated taxa by Day 30 on the IMM-substrates and IMM-substrate area closely paralleled the slope of the relationship between the number of taxa on Day 30 COL-substrates and COL-substrate area (Figure 11). COL-substrate taxa numbers, therefore, accurately

reflected cumulative immigration for all substrate sizes. Parallelism in slopes alone, however, overemphasizes the influence of the immigration pool in forming communities. Relative abundances of several major taxa were not representative of random sampling from the invasion pool (Table 10). Chironomidae was relatively more abundant on Day 30 COL-substrates than on IMM-substrate immigration pools. The opposite was true for Simuliidae, Ephemeroptera, and Hydracarina. Interactions (mostly undefined) must be occurring.

Part III is an examination of community formation from one end of a random - deterministic spectrum. Communities will be constructed (through computer simulation) by random processes of immigration and extinction, with as few constraints as possible. Communities constructed in this manner will then be compared to actual macroinvertebrate communities on stream rocks in order to evaluate the importance of random processes in determining community structure.

### PART III

#### METHODS

Before constructing communities by random processes, daily limits had to be set as to the number of individuals which a substrate could support on a given day during colonization (i.e. its carrying capacity); these limits should have biological significance. Average numbers of individuals found on COL-substrates served as good estimates of carrying capacity for Days 2, 4, 10, 19, and 30. Limits, however, were needed for each of the 30 days. The increase in carrying capacity between sampling dates was assumed to be linear. All runs were performed with MEDIUM-COMPLEX substrate immigration and colonization data found in Part II.

Random selection and extinction processes were performed as follows:

- 1) For Day 1,  $K_1$  number of individuals were randomly selected from the Day 1 immigration pool, where  $K_i$  is the number of individuals that can be supported on a given day ( $i$ ).

- 2) Before proceeding to Day 2, a certain percentage of the Day 1 community underwent random extinction. The extinction intensities (the percentage of the community going extinct at random) were set, a priori at three different levels: 5, 10, and 20% extinction. One intensity was used for each run (a run consisting of 30 "days" of colonization). Any fractions were rounded up to the nearest whole integer (because a fraction of an individual cannot go extinct). For example, the average  $K_1$  for a MEDIUM-COMPLEX COL-substrate community on Day 1 was 6 individuals. Therefore, 6 individuals were selected at random from the Day 1 immigra-

tion pool (obtained from the IMM-substrate sampling on Day 1). Before proceeding to Day 2, 5% of the Day 1 community underwent random extinction because  $0.05 * 6 = 0.3$ , 1 individual from the 6 was randomly selected for extinction.

3) For a Day 2 community, individuals were again selected from the Day 2 immigration pool to replace individuals lost due to extinction (on Day 1) and to add individuals in order to reach the new carrying capacity,  $K_2$ . In the example,  $K_2 = 12$ . Because the Day 1 community has 5 individuals (one went extinct), 7 individuals were selected from the immigration pool (in order to reach 12 individuals). If the demand for individuals by the present community exceeded the number of individuals in the immigration pool, the entire immigration for the following day was added. Sometimes, therefore, a community failed to reach carrying capacity, especially at high extinction intensities where large numbers of extinct individuals had to be replaced in addition to adding more individuals to reach the new carrying capacity. Failure to reach  $K_i$  resulted in declining growth rates.

4) The above steps were repeated every day, through Day 30.

Simulated communities were then analyzed in the same manner as COL-substrate communities. Immigration and extinction rates were calculated. Simulated colonization should have higher rates of immigration and extinction because all turnovers can be observed. It should be noted that once a taxon emigrated from the simulated substrate, its reappearance was considered a true immigration. High turnover of taxa would create high immigration rates. Extinction could occur at two locations in the

model. First, taxa in the daily immigration pools which are not present on the substrate community and are not randomly selected to colonize the simulated substrate (Step 1 above) constitutes an extinction. Second, colonists were randomly selected for extinction (Step 2 above).

Two important assumptions are implicit in the model. These are:

- 1) Each individual has an equal impact on the community, with each individual requiring the same amount of space and other resources.
- 2) Selection of immigrants and extinction of colonists was totally random, i.e. each individual had equal chances at becoming a colonist and at going extinct (after becoming a colonist).

It is difficult to assess the importance of assumption 1. If large individuals consistently appear in the immigration pool, the carrying capacity of the substrate community will be lowered (assuming space is limiting). A more sophisticated model could consider each individual extinction as available space rather than as a missing individual. In this way, vacant space could be "filled" in several different ways (e.g. one large Hydropsyche or several small Chironomidae).

Assumption 2 was a great simplification of the real world. Empty slots (individuals for the simulation being a "slot") are filled at random from the immigration pool. Non-random extinction has already occurred, because individuals in the immigration pool are not random samples from the drift. However, this non-random selection has been incorporated into the definition of immigrant by including only those taxa adapted for some potential success at colonization. A completely random simulation with respect to immigration would randomly select individuals from the passing drift, with daily drift serving as the immigration pool.

It is at this junction where the simulations seem counter intuitive to the real world. Each individual, regardless of which taxon it belongs to, has equal probabilities of extinction. Yet in Part II, tendencies for extinction varied among different taxa groups. It would seem that more abundant taxa are successful colonists because they are best adapted for the present conditions (though not necessarily true). An individual belonging to a successful taxon should have lower extinctability. Within the structure of this model, a taxon's extinctability is proportional to its relative abundance in the community and immigration pool. With high relative abundance in the immigration pool, taxon's rescue potential is high. If extinction probabilities could be adjusted at the level of the individual (with each taxon having its own probability of extinction for each individual), a more realistic model would follow. However, this simple model provides a chance to examine the role of random processes in determining community structure with few limitations.

### PART III

#### RESULTS AND DISCUSSION

All three extinction intensities produced colonization curves within the 90% confidence limits on taxa number found in each sampling interval for MEDIUM-COMPLEX COL-substrate communities (Figure 14). Increasing extinction intensities produced much more erratic colonization curves. In comparing colonization rates (for each sampling interval), simulated communities with an extinction intensity of 0.05 had colonization rates most similar to MEDIUM-COMPLEX COL-substrates, although the 0.10 intensity also was close. Growth rates were closest with the 0.05 intensity (Table 11). Other extinction intensities, especially 0.20, greatly reduced the size of Day 30 communities, i.e. daily immigration pools were not large enough to absorb a 20% loss in individuals (each day), and yet, keep pace with the continually rising carrying capacity.

Immigration rates (Table 11) were predictably higher because all immigrations could be monitored, including the increase in immigration due to turnover within sampling intervals. Once taxa became extinct, their reappearance in the immigration pool constituted an immigration; this was undetectable for COL-substrate colonization. Extinction rate, due to the observable turnover, also was higher for the simulations (Table 11). Surprisingly, 0.20% simulations had lower extinction rates up until the last sampling interval. This was due to high replacement of taxa (Table 11) by the immigration pool. With 20% of the individuals emigrating each day, most taxa in the daily immigration pool were selected for colonization (in order to keep pace with  $K_i$ ), thereby intro-

Figure 14. Cumulative colonization curves for simulated MEDIUM-COMPLEX substrate communities with 5, 10, and 20% extinction intensities. The 90% confidence interval on taxa numbers for each interval for MEDIUM-COMPLEX COL-substrate communities is provided for comparison.

- (a)...5% extinction intensity
- (b)...10% extinction intensity
- (c)...20% extinction intensity

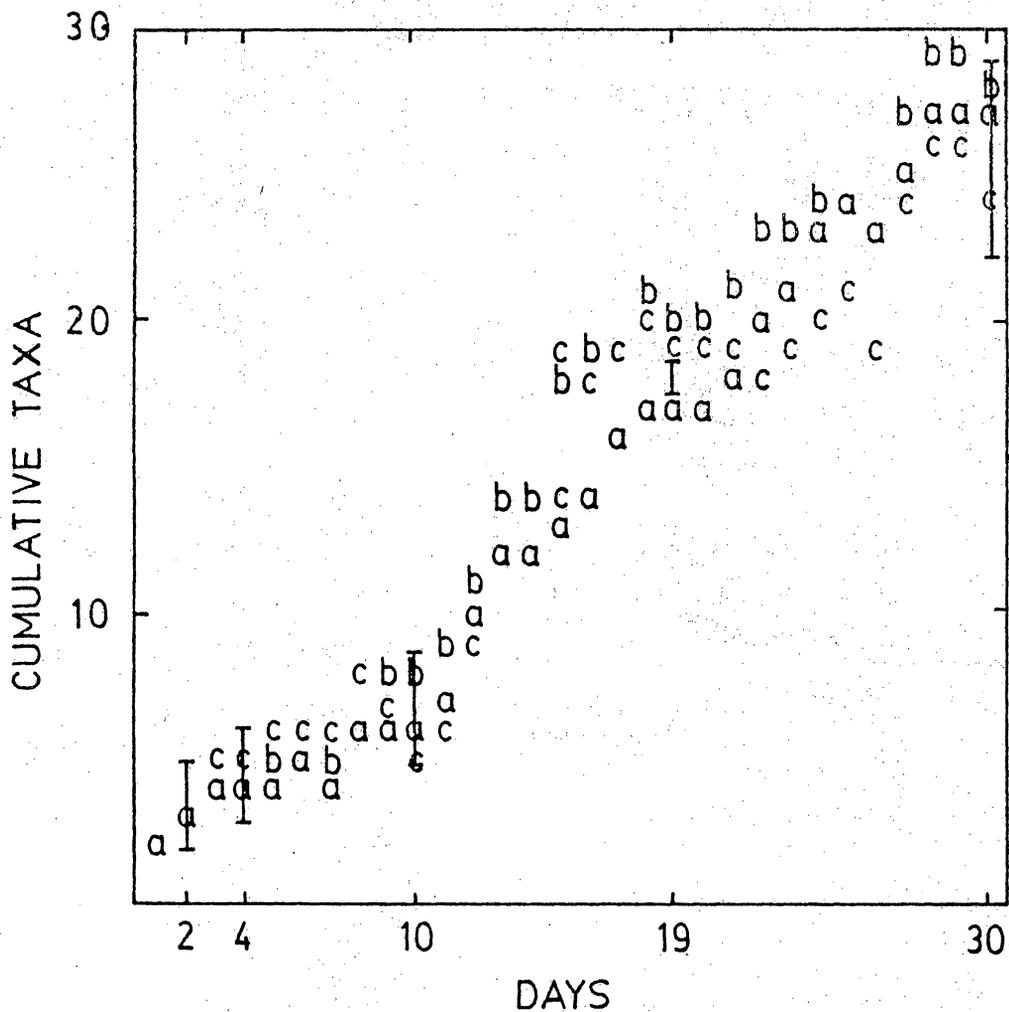


Table 11. Immigration rate (new taxa / Day), extinction rate (extinct taxa / Day), colonization rate (colonizing taxa / Day), and growth rate (added individuals / Day) in each sampling interval for simulated MEDIUM-COMPLEX COL-substrate communities with 5, 10, and 20% extinction intensities.

0.05 Extinction					
Rate	Days				
	1-2	3-4	5-10	11-19	20-30
Immigration	2.00	2.00	1.17	2.11	1.27
Extinction	0.50	1.50	0.83	0.89	0.36
Colonization	1.50	0.50	0.33	1.22	0.91
Growth	5.50	0.00	1.17	9.44	23.82

0.10 Extinction					
Rate	Days				
	1-2	3-4	5-10	11-19	20-30
Immigration	2.00	2.00	1.17	2.00	1.18
Extinction	0.50	1.00	0.67	0.67	0.55
Colonization	1.50	1.00	0.50	1.33	0.64
Growth	5.50	0.00	1.17	8.89	17.45

0.20 Extinction					
Rate	Days				
	1-2	3-4	5-10	11-19	20-30
Immigration	2.00	2.00	1.00	2.11	1.91
Extinction	0.50	1.00	1.00	0.56	1.45
Colonization	1.50	1.00	0.00	1.56	0.45
Growth	5.50	0.00	1.00	6.56	11.00

ducing new taxa (usually rarer taxa) and rescuing any taxa lost by random extinction.

Several runs of 0.05 extinction intensity produced communities with similar taxa compositions. Taxa overlap was never below 90 per cent. This indicated that random processes of immigration and extinction might not be responsible for the low overlap in taxa composition for COL-substrate communities or communities on rocks. Rather, each substrate (and rock) may intercept a substantially different immigration pool. This would cause much greater dissimilarity in taxa composition among "islands".

Dominance-diversity curves were similar among simulated and between simulated and COL-substrate communities. However, simulated communities had 3 to 4 taxa with relative abundances above 0.10, rather than 1 or 2 taxa for COL-substrate communities. Simulated communities more closely reflected the structure (relative abundance of major taxa groups) of the immigration pool than COL-substrate communities (Day 30) (Table 12). The greater deviation in taxa relative abundances between COL-substrate communities (Day 30) and the immigration pool compared to the smaller deviation between simulations and immigration pools indicated an interaction either between organism and environment or between organisms which shaped community structure of the COL-substrate communities, at least partially independent of random selection from the immigration pool (compare Table 12 to Part II).

An important observation while performing these simulations was that no taxa went extinct if 3 or more individuals managed to colonize

Table 12. Relative abundances of major taxa groups in simulated communities for Day 30.

Taxon Group	Extinction Intensity		
	0.05	0.10	0.20
Chironomidae	0.649	0.685	0.599
Hydracarina	0.173	0.173	0.248
Ephemeroptera	0.071	0.038	0.055
Trichoptera	0.019	0.020	0.005
Mollusca	0.006	0.010	0.005
Simuliidae	0.077	0.058	0.061

the substrate. Though a taxon's low extinctability was proportional to its relative abundance in the community and, partially, in the immigration pool (better chance of a rescue effect), an extinction intensity of 20% was not sufficient to lead to the extinction of any but the rarest taxa. Also, as the total population size of the entire community increased with time, chances of random extinction for a very rare taxon (an abundance of 1 individual) decreased, though still higher than more common taxa. Therefore, rare taxa were sheltered from rapid stochastic extinction by being a member of a large community. For example, in a simulated community with a 0.05 extinction intensity, a rare taxon had a 0.049% chance of extinction on Day 30 and a 0.056% chance of extinction on Day 10. The abundance of rare taxa in COL-substrate communities may be the result of statistical sheltering if random extinction is commonplace. By the time random extinction could occur, a taxon stands a good chance of being rescued by the immigration pool.

### PART III

#### SUMMARY

Simulations, especially with a 0.05 extinction intensity, closely mimicked COL-substrate colonization though distorting relative abundance patterns of certain taxa. Stochastic processes of immigration and extinction, therefore, may be of considerable importance (though not the total process) in directing stream invertebrate colonization. A recent article by Simberloff (1978) stressed that stochastic colonization, rather than large scale competition, can account for observed biogeographic patterns in distributions. On a smaller scale, the colonizations of stream rocks appear to be, in large part, stochastic.

PART IV  
Plans  
for the  
Coexistence of Taxa  
in  
Stream Invertebrate Communities

GENERAL DISCUSSION

How do stream benthic invertebrates coexist on a single rock? Only by trying to understand how species populations partition space among themselves, can we begin to evaluate the importance of area and surface complexity in determining population sizes and taxa numbers. Any spatial-diversity hypothesis must account for the extreme variability in taxa composition (see overlap data in PARTS II and I). This discussion will be directed towards positing three plans for coexistence and then, with each plan, describing how area and complexity could affect macrobenthic diversity.

Plan I

Suppose each taxon requires its own exclusive microhabitat in order to successfully colonize a given rock. In other words, the competitive exclusion principle is fully operative with regard to space such that one taxon can best utilize any given location on the rock surface. Thus, if our knowledge of stream organisms were sufficiently developed to completely outline and measure the factors controlling each species' realized niche, a rock surface (at any given time of the year) could be mapped out assigning each position to one taxon. The process of colon-

ization would then be a simple juggling of taxa until the proper taxa were settled in their respective microhabitats.

Space, by itself, is meaningless as a resource for which species compete. Space is a multi-factor variable (Minshall and Minshall, 1977). It is the range of velocities found over the surface, the amount of light reaching the surface, the frequency of visits from nearby predators, etc. which makes a given space desirable and worth competing for. Ultimately a benthic organism must secure space to survive, but it is the combinations of these environmental and biotic factors at a given location on the rock which will determine its success. Plan I contends that species exclude one another by specializing on a unique combination and range of factors at which no other species could persist. Locations in space where persistence is likely are called microhabitats, i.e. the combination of all factors at a given point on the surface creates a space at which only one species' realized niche could exist. Rocks of the same shape and size found in the same physical environment should, according to Plan I, have the same number and types of taxa because each location on the surface of all the rocks would provide the same microhabitats.

Before discussing the validity of Plan I, how would area and/or complexity regulate macroinvertebrate diversity? I initially hypothesized that surface complexity would be closely correlated with taxa diversity because rocks of greater complexity would have more types of microhabitats. This was not the case; area was a much better predictor of diversity (PART I). The presence or absence of a particular taxon, however,

would be dependent upon more than having its microhabitat present on the rock surface. Each taxon's microhabitat must be sufficiently abundant to support a critical population size, partially insuring some immunity from random extinction. An increasing population size with area can only be supported provided microhabitat availability is increasing at a proportional rate with area. Thus, to increase the availability of a specific taxon's microhabitat (and increase its population size) a rock must either be "made" more complex for the taxon being considered or rock area must be increased, keeping the original degree of surface complexity constant for every increase in area. The first alternative would decrease the abundance of other microhabitats by changing complexity in favor of one taxon. Preferably, the second alternative would lower extinction rates for all taxa by increasing the abundance of microhabitats already present. Formerly scarce microhabitats could then be more frequent, supporting critical population sizes and raising overall taxa numbers.

The roles of area and complexity in affecting diversity are inseparable. The quantification of surface complexity functions as a measure of habitat richness and relative abundance of microhabitats while area functions as a measure of absolute abundances of microhabitats. Interpretation of species numbers trends with increasing area could be reinterpreted as a species diversity trend with increases in spatial heterogeneity. Smith (1972) defined heterogeneity by stating, "An environment is heterogeneous to a process if the rate of the process varies over space in relation to structural variations of the environment, and

homogeneous to a process that does not vary in this fashion." The process, an accumulation of species, varies (increasing  $S$  with greater island area) because more microhabitats become available. Availability is a product of both area and surface complexity, together.

The evidence from PART I does not support Plan I as developed above. Taxa overlap (B) values were low for communities found on rocks of similar area and complexity (Appendix II); even under the more rigid environmental control of substrate colonization in PART II overlap was low (Table 6). These results cannot be interpreted as unequivocal proof that Plan I was false; other mechanisms can be postulated that would create dissimilarity among rock communities found in identical environments and yet would not violate the framework of Plan I.

In the description of microhabitats, "locations" were never assigned real dimensions (length, width, and height). Because stream organisms obviously require more than an abstract location within which to exist, actual microhabitat size must be assigned a real space on the rock surface. Microhabitat size would be a function of the identity and proportional to the size of the immigrating individual. Larger individuals of the same taxon require more space, thus lowering the number of available microhabitats on the rock surface.

Variability in size within a species usually has a very minor effect on relative abundance patterns and carrying capacity of individuals. For example, size variation within individuals in the dove guild on New Guinea (see Diamond, 1975) would not dramatically change community composition for the entire island. Birds and their variations in size with-

in the guild are relatively small in comparison to the island. For stream rocks, however, colonizing organisms are much larger relative to the rock. A large hydropsychid larvae on a small rock (e.g. 8 cm in diameter) is "equivalent" to an organism 540 km long colonizing New Guinea (2880 km). Such an organism would have a profound effect on any island's community structure. Additionally, Hydropsyche larvae varied in their length by a factor of 10. Variability on the order of a 5 to 10 fold difference was found for other taxa as well (e.g. Simulium, Baetis, and Epeorus). Because all organisms require space, other than that to rest their bodies, for other functions such as grazing, a substantial proportion of the rock surface could be greatly affected by a large individual, especially on SMALL rocks. This same space could have been occupied by several smaller individuals of the same species if they had colonized first (and were able to defend that space). Stochasticity, therefore, in the order of appearance of different sized individuals of the same species in the drift could alter community structure, even for rock communities with identical physical environments.

Macroinvertebrate stream communities are composed of a wide variety of organisms, spanning several phyla. Size differences among mature larvae or adults of different taxa in Sinking Creek are dramatic (e.g. 0.5 mm chironomids compared to caddisflies 2.1 cm long or relatively massive snails). Each member of a stream community must recognize a slightly different level of complexity for the same rock surface as the result of differences in size and behavior. The same section of surface may be spatially heterogeneous (coarse-grained) for one size class per-

mitting those taxa to subdivide space through competitive exclusion, while the same surface could be homogeneous (fine-grained) for larger taxa classes permitting those taxa to subdivide on a limited basis. A consequence of this arrangement is that a surface providing unique microhabitats for smaller organisms may be encompassed within a single microhabitat space for a large organism. If the larger organism locates this space first, the smaller organisms (possibly comprising several taxa) could be excluded. While large taxa may passively exclude smaller taxa by simply occupying their microhabitat space, predation and active competition for similar food could exclude smaller taxa (see Wilson, 1975). Again, chance in the order of arrival of potential colonists could determine the partitioning of space and influence overall community structure.

Plan I requires that each species be highly specialized. This, however, is unlikely; stream macroinvertebrates are predominantly generalists (Cummins, 1973; Patrick, 1975). In order to secure food, a benthic organism must first secure space. These two resources, food and space, must be subdivided to some extent in order for many species to at least temporarily coexist. Cummins (1973) concluded that most species are food generalists, eating essentially what is there. However, there are examples of food particle size partitioning and of food preferences (Hynes, 1970). There should, however, be a limit to effective partitioning of food. Because space, the other resource in demand, is a product of many variables (as discussed earlier), specialization is actually based on tolerances to the physical environment and an ability

to defend acquired space. Again, evidence can be found where congeneric species each specialize on certain ranges of velocity (Edington, 1968) or have preferred positions on substrates (Maitland and Penny, 1967; Hynes, 1970; Kovalek, 1976). Morphological variations in body form and mouthparts are also evidence of specialization to certain parameters in the environment (see Hynes, 1970). Certainly, most species are adapted to some extent for tolerating certain ranges of environmental factors and utilizing different types and sizes of food. However, these tolerances are broad with substantial overlap in utilization among many species. Even among congeneric species overlap is broad. For example, Grant and Mackay (1969) concluded that many of the congeneric species in their study had similar microhabitat requirements but staggered emergence periods, limiting competition to times of temporal overlap.

#### Plan II

Rather than interpreting the rock surface as a collection of discrete microhabitats, the surface can instead be interpreted as a mosaic of broad habitat types. The basic difference between Plan I and II is that in Plan II the microhabitats of several species are extremely similar, making survival at a given surface location the same for several taxa. Areas with a fairly homogeneous exposure to a given range of environmental factors will provide the necessary habitat for several taxa. These areas can be called patches (Levin and Paine, 1974). Examples of patches can be barren upper surfaces on rocks exposed to a fast current, creviced surfaces with smooth sides on the crevice faces with a swift current flowing above, or the same surface with a slow current above.

Plan II, as in Plan I, assumes considerable behavioral and trophic interaction between community members. Thus, as each potential colonist arrives at a patch:

- 1) first, it occupies space, limiting the number of colonists to be added to the patch.

- 2) through species interactions, it partially determines which species will successfully colonize in the future.

As more and more individual colonists arrive, the sets of immigrating species which will successfully coexist with established colonists becomes greatly reduced (i.e. certain combinations of species cannot coexist due to competition and predation). As in Plan I, the sequence in arrival of immigrants may directly affect overall community structure.

Complexity and area effects for Plan II are similar to Plan I, only now, complexity is an indirect measure of patch type and relative abundance. An additional effect may occur. As patches become large, two species adapted for a particular patch which are highly antagonistic, could temporarily coexist by occupying extreme ends of the patch thereby avoiding physical contact. Rarer species that may be competitively inferior at retaining space or avoiding predation can survive in this manner. Rare species can also occupy areas between patches where few species have the ability to permanently reside.

Through an interpretation of Plan II, a rock is actually a collection of mini-islands, with each patch being an island. The diversity of communities on rocks would then be the sum of all species among the patches.

The plausibility of Plan II depends upon the degree of interaction among stream invertebrates. The most overt form of interaction is that of predation (see Cummins, 1974 and 1975; Hynes, 1970). For the other form of interaction, competition, two extreme types are recognized. Interference competition is where one species limits utilization of a resource by another species through territoriality or aggression (Jaeger, 1974). Exploitation is where one species is better adapted at attaining a limiting resource, thereby obtaining a greater proportion of it (see Miller, 1969). Both these extremes are exhibited by stream invertebrates to varying degrees. In commenting on a paper by Miller (1967), Jaeger (1974) noted that "for interference competition to occur, there must be some form of intraspecific communicatory mechanism, such as territoriality, that has been extended to interspecific interactions. Organisms that have not evolved such systems are not likely to resort to interference to resolve conflicts over resources." Corkum (1978) found that as space became limiting Paraleptophlebia mollis used intraspecific aggression to control spacing between individuals while Baetis vagans simply lifted off from the substrate when densities became high. Both species, therefore, exhibit a divergence in the two strategies of competition. The exact spacing of simuliid larvae over a smooth surface (Zahar, 1951) or the intraspecific aggression among caddis larvae observed by Glass and Bovberg (1969) could also lead to interference competition. Both Plan I and Plan II rely heavily on interference since this is a mechanism which immediately exerts control over how many individuals and which species may coexist, especially as space becomes

limiting. Exploitation, on the other hand, may take many generations to be effective at limiting certain taxa populations and would not exert an obvious control over determining which taxa will coexist over a very short time (several days to two months), which is the primary time scale of concern in this discussion. Unfortunately, evidence of exploitation is difficult to obtain. Most stream organisms are, however, thought to be opportunistic (Patrick, 1975), probably utilizing exploitation rather than solely interference strategies.

Both Plans I and II treat macroinvertebrate community formation deterministically with randomness, the incomplete overlap in taxa composition between environmentally similar rock communities, existing only because the immigration pools (mainly drift) are variable for each rock. An interactive equilibrium is implied for both plans with species populations existing near carrying capacity, forcing interactions (intra- and interspecific). However, for an equilibrium to survive (even temporarily) physical disturbance must be kept to a minimum. A constantly fluctuating physical and biotic environment would continually change types and distributions of microhabitats and/or patches and would, consequently, continually select for different sets of species (Hutchinson, 1975; Connell, 1978; Weins, 1977). If change occurred rapidly, there would be a constant lag in response by the macrobenthic community resulting in many species coexisting in disequilibrium. An important question, then, in evaluating the potential reality of either plan is not only whether a high degree of interaction exists but also whether all species become resource limited, forcing interaction with one

another to the point of active exclusion. The observed physical variability (temporal and spatial) of streams by many researchers (e.g. Patrick, 1975), along with the widespread patchy distribution of most species found in the experiment all suggest a highly variable environment. A variable environment and predominantly generalist species are not conducive for having communities structured on a high degree of interaction based on competitive exclusion (see Hutchinson, 1975, for some interesting comments).

### PART III

The foundation of this plan was derived from the following:

"The existence of high local diversity in the face of such overlap in resource requirements is a problem only if one assumes equilibrium conditions. Discard the assumption and the problem vanishes." (Connell, 1978, p.1309)

Nonequilibrium characterizes Plan III and closely parallels, in part, a similar model proposed by Sale (1977) and Sale and Dybdahl (1978).

Plan III does retain some of the characteristics of previous plans. The concept of a patch network over the rock is preserved, i.e. there are broad habitat types on the rock surface. This again implies that stream taxa are specialized to some extent with most species capable of only occupying a subset of all patch types. Area and complexity effects on species are also the same as Plan II. Unlike Plan II, once an individual has vacated space on the surface, it is replaced, at random, by an individual from the pool of immigrants which could survive in that patch. Interactions between taxa are not considered to be important in determining the success of an immigrant. Sale (1977) described his model

as a "lottery for living space in which larvae (of coral reef fish) are tickets and the first arrival at a vacant site wins that site. The lottery operates within habitats and at the level of the individual fish." The species composition of a given patch (and, collectively, of the entire rock) would depend upon chance colonization with individuals, selected at random from the pool of immigrants, colonizing available space within each patch.

In Plan III, the probability of extinction for each individual colonist is considered to be the same, regardless of taxon. This plan assumes that extinction of a species (and, therefore, of individuals) is independent of time and intra- and interspecific population densities. With immigration and extinction occurring stochastically, the composition of the immigration pool should greatly influence the structure of a community fashioned after Plan III.

The simulations in Part III provided a test of Plan III. The results indicated that although simulated communities had similar taxa numbers at the end of 30 days, their relative abundance structures differed from real substrate communities. Nonrandom immigration and /or extinction among taxa was important.

#### Evaluation of Plans

Three plans have been proposed. All three consider at least some specialization to the environment for most taxa but each plan varies considerably in the degree of assumed presence or importance of interactions (especially competition). The natural question, of course, is which plan best describes the partitioning and regulation of space in

macroinvertebrate stream communities within the narrow time frame of approximately 6 to 8 weeks on individual rocks (i.e. a question of maintenance of high local diversity in ecological time). An answer is not simple.

Because most taxa are considered to be generalists (as discussed earlier), competitive exclusion to the extreme in Plan I where all members in the community effectively exclude one another is very unlikely. Plan I would not be appropriate for entire rock communities but may account for the presence of certain taxa. Very high, laminar flows over smooth surfaces are often shared only by Simulium and Blepharicera, though Baetis was found to quickly forage over the surface but within seconds return to sheltered areas. Exclusion of most taxa, therefore, can occur at combinations of extreme environmental factors.

The basic difference between Plans II and III centers on the mode of extinction. In Plan III, extinction occurs at random, unaffected by taxa types, time, or population densities; each immigrant has the same chance of being a colonist and the same chance, once established, of going extinct. In Plan II, extinction is non-random both for immigrating individuals and colonizing immigrants. Interactions among colonists permit only certain individuals (and, therefore, taxa) to colonize. Turnover of individuals would be much lower in a Plan II type community, provided the physical environment of the surface did not change and alter the competitive advantages of the established colonists. I can only infer as to which plan is best because our knowledge of how and where extinction occurs is very limited.

I hypothesize that a hybrid of Plans II and III, leaning towards Plan III, provides the most realistic model. The invasion of available space is random (as described by Sale, 1977, for fish) with the success of an invading individual being independent of the colonists surrounding it (except if the nearby colonist is a hungry predator). Immigrants landing in space occupied by an organism recognizing the same environmental grain, quickly emigrate (i.e. giving the resident the competitive advantage). Immigration, therefore, only occurs when space is vacant. As a rock community approaches equilibrium, extinction of newly arriving immigrants increases because available space becomes limiting. Colonists also undergo extinction during this period in the following ways:

- 1) Competitive interactions, both inter- and intraspecific, which gradually increase as population densities become dense.
- 2) Gradual shifts in the substrate environment which alters competitive abilities of many taxa.
- 3) Random extinction, such as the tumbling of the rock during a storm which scrapes off algae and animals.

Relative importances of the three are unknown. During an approach to an equilibrium (as in this experiment), organism-environment interactions are probably most important. As equilibrium is attained (and after), organism-organism interactions and random events would account for high extinction. Extinction, therefore, is interpreted as being a non-random process though the actual form of extinction is uncertain. If a particular rock or substrate is permitted to have its invertebrate community

undergo colonization for an extended period of time (60 days or more), the structure of the community (relative abundance of major taxa) would continue to deviate from the structure of the immigration pool due to non-random extinction. COL-substrate communities (Day 30) began to show this trend.

## CONCLUSIONS

1. A taxa number-area relationship does exist for invertebrate communities found on stream rocks or artificial substrates. Larger rocks or substrates support more taxa.
2. COMPLEX rock surfaces or artificial concrete substrate surfaces support more diverse communities than rocks of simpler surfaces with identical areas. SIMPLE rocks, however, exhibit a greater rate of increase in taxa number with area because, hypothetically, a series of SIMPLE rocks has a greater rate of increase in the abundance and types of microhabitats with increasing rock area, than a series of COMPLEX rocks.
3. Taxa number-rock area slope estimates cannot be compared to Preston's 0.27 estimate because the underlying assumptions are unrealistic when applied to stream invertebrate communities on rocks; all dominance-diversity relationships for communities on rocks do not approximate a lognormal distribution and population size per unit of area does not remain constant with rock area.
4. Most taxa are not restricted to certain rock or substrate sizes or surface complexities, though both factors will influence population size.
5. Communities on larger substrates or substrates with more complex surfaces have higher overall immigration, invasion, replacement, and colonization rates. During colonization, these rates are not monotonic functions with time.
6. Extinction is constant with area during the first 30 days of colonization (assuming constant turnover with area).

7. Algal colonization (during early community development, up through 30 days) creates more types and numbers of microhabitats for immigrating macroinvertebrate taxa, thus lowering extinction and raising invasion and immigration rates for most taxa (especially for the Chironomidae and Hydracarina). Thick algal mats make SIMPLE and COMPLEX surfaces ecologically similar. Algal colonization is a fundamental factor in determining stream community equilibria.

8. Substrate communities do not reach (in Sinking Creek) an equilibrium in numbers within 30 days of colonization (starting with an initially barren surface).

9. Individuals in stream macroinvertebrate communities on rocks are not random samples from the immigration pool. Interactions, of some kind, are fundamental in shaping community structure (and, therefore, taxa number).

## LITERATURE CITED

- Allan, J.D. 1975. The distributional ecology and diversity of benthic insects in Cement Creek, Colorado. *Ecology* 58:1040-1053.
- Barr, J. A., J. H. Goodnight, J. P. Sall, and J. T. Helwig. 1976. A user's guide to SAS 76. SAS Institute Inc., Raleigh, N. C.
- Brown, J. H. and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: Effect of immigration on extinction. *Ecology* 58:445-449.
- Calow, P. 1972. A method for determining the surface areas of stones to enable quantitative density estimates of littoral stone-dwelling organisms to be made. *Hydrobiologia* 40:37-50.
- Christiansen, F. B. and T. M. Fenchel. 1977. Theories of populations in biological communities. Springer-Verlag, New York, New York.
- Connell, J. H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. In M. L. Cody and J. M. Diamond, eds., *Ecology and evolution of communities*. Belknap Press of Harvard University, Cambridge, Mass.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302-1310.
- Corkum, L. D. 1978. The influence of density of behavioural type on the active entry of two mayfly (Ephemeroptera) into the water column. *Can. J. Zool.* 56:1201-1206.
- Cummins, K. W. 1974. Structure and function of stream ecosystems. *Bioscience* 24 (11):631-641.
- Cummins, K. W. 1975. Macroinvertebrates. In B. A. Whitton, ed., *River ecology*. Blackwell Scientific Publ., Oxford.
- Dahl, A. L. 1973. Surface area in ecological analysis: quantification of benthic coral-reef algae. *Mar. Biol.* 23:239-249.
- Darlington, P. J. 1972. Competition, competitive repulsion, and coexistence. *Proc. Nat. Acad. Sci. U. S. A.* 69:3151-3155.
- Dazo, B. C. 1965. The morphology and natural history of *Pleurocera acuta* and *Goniobasis livescens* (Gastropoda: Cerithiacea: Pleuroceridae). *Malacologia* 3 (1):1-80.

- de March, B. G. E. 1976. Spatial and temporal patterns in macrobenthic stream diversity. *J. Fish. Bd. Can.* 33:1261-1270.
- Dickson, K. L. and J. Cairns. 1972. The relationship of freshwater macroinvertebrate communities collected by floating artificial substrates to the MacArthur-Wilson equilibrium model. *Am. Midl. Nat.* 88 (1):68-75.
- Diamond, J. M. 1969. Avifaunal equilibria and species turnover rates on the Channel Islands, California. *Proc. Nat. Acad. Sci. U. S. A.* 69:3199-3203.
- Diamond, J. M. 1972. Biogeographic kinetics: Estimation of relaxation times for avifaunas of Southwest Pacific Islands. *Proc. Nat. Acad. Sci. U. S. A.* 69:3199-3203.
- Diamond, J. M. and E. Mayr. 1976. Species-area relation for birds of the Solomon Archipelago. *Proc. Nat. Acad. Sci. U. S. A.* 73 (1): 262-266.
- Edington, J. M. 1968. Habitat preferences in net-spinning caddis larvae with special reference to the influence of water velocity. *J. Animal Ecol.* 37:675-692.
- Friberg, F., L. M. Nilsson, C. Otto, P. Sjoström, B. W. Svensson, Bj. Svensson, and S. Ulfstrand. 1977. Diversity and environments of benthic invertebrate communities in Swedish streams. *Arch. Hydrobiol.* 81 (2):129-154.
- Fox, L. R. 1977. Species richness in streams - an alternative mechanism. *Am. Nat.* 111:1017-1021.
- Gilroy, D. 1975. The determination of the rate constants of island colonization. *Ecol.* 56:915-923.
- Glass, L. W. and R. V. Bovbjerg. 1969. Density and dispersion in laboratory populations of caddisfly (Cheumatopsyche, Hydropsychidae). *Ecol.* 50:1082-1084.
- Glime, J. M. and R. M. Clemons. 1972. Species diversity of stream insects on Fontinalis spp. compared to diversity on artificial substrates. *Ecol.* 53:458-464.
- Grant, P. R. and R. J. Mackay. 1969. Ecological segregation of systematically related stream insects. *Can. J. Zool.* 47:691-694.
- Harner, R. F. and K. T. Harper. 1976. The role of area, heterogeneity, and favorability in plant species diversity of Pinyon-Juniper ecosystems. *Ecol.* 57:1254-1263.

- Hobbs, R. S. 1975. "Spatial and temporal distributions of selected immature aquatic insect species in Sinking Creek, Virginia." M. S., Virginia Polytechnic Institute and State University.
- Hollander, M. and D. A. Wolfe. 1973. Nonparametric statistical methods. Wiley Series in Probability and Mathematical Statistics, John Wiley and Sons, New York, New York.
- Hutchinson, G. E. 1965. The ecological theater and the evolutionary play. Yale University Press, New Haven.
- Hutchinson, G. E. 1975. Variations on a theme by Robert MacArthur. In M. L. Cody and J. M. Diamond., eds., Ecology and evolution of communities. Belknap Press of Harvard University, Cambridge, Mass.
- Hynes, H. B. N. 1970. The ecology of running waters. University of Toronto Press, Toronto.
- Jaeger, R. G. 1974. Competitive exclusion: comments on survival and extinction of species. Bioscience 24:33-39.
- Kovalek, W. P. 1976. Seasonal and diel changes in the positioning of Glossosoma nigrior(Trichoptera: Glossosomatidae) on artificial substrates. Can. J. Zool. 54:1585-1594.
- Kovalek, W. P. 1978. Diel changes in stream benthos density on stones and artificial substrates. Hydrobiologia 58:7-16.
- Lassen, H. H. 1975. The diversity of freshwater snails in view of the equilibrium theory of island biogeography. Oecologia 19:1-8.
- Levin, S. A. and R. T. Paine. 1974. Disturbance, patch formation, and community structure. Proc. Nat. Acad. Sci. U. S. A. 71:2744-2747.
- Linduska, J. P. 1942. Bottom type as a factor influencing the local distribution of mayfly nymphs. Can. Entomol. 74:26-30.
- Lium, B. W. 1974. Some aspects of aquatic insect populations of pools and riffles in gravel bed streams in Western United States. J. Res. U. S. Geol. Survey 2 (3):379-384.
- Lynch, J. F. and N. K. Johnson. 1974. Turnover and equilibria in insular avifaunas with special reference to the California Channel Islands. Condor 76:370-384.
- MacArthur, R. H. 1972. Geographical ecology: patterns in the distribution of species. Harper and Row, New York, New York.

- MacArthur, R. H., J. W. MacArthur, and J. Preer. 1962. On bird species diversity. II. Prediction of bird censuses from habitat measurements. *Am. Nat.* 96:167-174.
- MacArthur, R. H. and E. O. Wilson. 1963. An equilibrium theory of insular zoogeography. *Evolution* 17:373-387.
- MacArthur, R. H. and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey.
- Maitland, P. S. and M. M. Penny. 1967. The ecology of the Simuliidae in a Scottish river. *J. Animal Ecol.* 36:179-206.
- May, R. M. 1975. Patterns of species abundance and diversity. In M. L. Cody and J. M. Diamond, eds., *Ecology and evolution of communities*. Belknap Press of Harvard University, Cambridge, Mass.
- Miller, R. S. 1967. Pattern and process in competition. *Adv. Ecol. Res.* 4:1-74.
- Miller, R. S. 1969. Competition and species diversity. *Brookhaven Symposia in Biol.* 22:63-70.
- Minshall, G. W. and J. N. Minshall. 1977. Microdistribution of benthic invertebrates in a Rocky Mountain (U. S. A.) stream. *Hydrobiologia* 55:231-249.
- Patrick, R. 1972. Benthic communities in streams. *Trans. Conn. Acad. Arts Sci.* 44:271-284.
- Patrick, R. 1975. Stream communities. In M. L. Cody and J. M. Diamond, eds., *Ecology and evolution of communities*. Belknap Press of Harvard University, Cambridge, Mass.
- Pearson, E. S. and H. O. Hartley, eds. 1972. *Biometrika tables for statisticians*. Vol. II. Cambridge University Press, Cambridge.
- Peet, R. K. 1974. The measurement of species diversity. *Ann. Rev. Ecol. Sys.* 5:285-307.
- Percival, E. and H. Whitehead. 1929. A quantitative study of some types of stream-bed. *J. Ecol.* 17:282-314.
- Pielou, E. C. 1975. *Ecological diversity*. John Wiley and Sons, New York, New York.
- Pinkham, C. F. A. and J. G. Pearson. 1976. Applications of a new coefficient of similarity to pollution surveys. *J. W. P. C. F.* 48: 717-723.

- Preston, F. W. 1962. The canonical distribution of commonness and rarity: Part I. and II. *Ecology* 43:185-215, 410-432.
- Sale, P. F. 1977. Maintenance of high diversity in coral reef fish communities. *Am. Nat.* 111:337-359.
- Sale, P. F. and R. Dybdahl. 1978. Determinants of community structure for coral reef fishes in isolated coral heads at lagoonal and reef slope sites. *Oecologia* 34:57-74.
- Sanders, H. L. 1968. Marine benthic diversity: a comparative study. *Am. Nat.* 102:243-282.
- Schoener, A. 1974. Colonization curve for planar marine islands. *Ecol.* 55:818-827.
- Scott, D. 1958. Ecological studies on the Trichoptera of the river Dean, Cheshire. *Arch. f. Hydrobiol.* 54:340-392.
- Seifert, R. P. 1975. Clumps of Heliconia inflorescences as ecological islands. *Ecol.* 56:1416-1422.
- Simberloff, D. S. 1974. Equilibrium theory of island biogeography and ecology. *Ann. Rev. Ecol. Syst.* 5:161-182.
- Simberloff, D. S. 1976a. Experimental zoogeography of islands: effects of island size. *Ecol.* 57:629-642.
- Simberloff, D. S. 1976b. Species turnover and equilibrium island biogeography. *Science* 194:572-578.
- Simberloff, D. S. 1978. Using island biogeographic distributions to determine if colonization is stochastic. *Am. Nat.* 112:713-726.
- Slobodkin, L. B. and H. L. Sanders. 1969. On the contribution of environmental predictability to species diversity. *Brookhaven Symposia in Biol.* 22:82-95.
- Smith, F. E. 1972. Spatial heterogeneity, stability, and diversity in ecosystems. *Trans. Conn. Acad. Arts Sci.* 44:307-335.
- Snedecor, G. W. and W. R. Cochran. 1967. *Statistical methods.* Iowa State University Press, Iowa City, Iowa.
- Stout, J. and J. Vandermeer. 1975. Comparison of species richness for stream-inhabiting insects in tropical and mid-latitude streams. *Am. Nat.* 109:263-280.

- Tepedino, V. J. and N. L. Stanton. 1976. Cushion plants as islands. *Oecologia* 25:243-256.
- Townsend, C. R. and A. G. Hildrew. 1976. Field experiments on the drifting, colonization and continuous redistribution of stream benthos. *J. Animal Ecol.* 45:759-772.
- Ulfstrand, S. 1967. Microdistribution of benthic species (Ephemeroptera, Plecoptera, Trichoptera, Diptera:Simulidae) in Lapland streams. *Oikos* 18:293-310.
- Ulfstrand, S., L. M. Nilsson, and A. Stergar. 1974. Composition and diversity of benthic species collectives colonising implanted substrates in a South Swedish stream. *Ent. Scand.* 5:115-122.
- Waters, T. F. 1972. The drift of stream insects. *Ann. Rev. Ent.* 17:253-272.
- Whittaker, R. H. 1972. Evolution and measurement of species diversity. *Taxon* 21:213-251.
- Wiens, J. A. 1977. On competition and variable environments. *Amer. Scientist* 65:590-597.
- Williams, D. D. and H. B. N. Hynes. 1976. The recolonization mechanisms of stream benthos. *Oikos* 27:265-272.
- Wilson, D. S. 1975. The adequacy of body size as a niche difference. *Am. Nat.* 109:769-784.
- Zahar, A. R. 1951. The ecology and distribution of blackflies (Simulidae) in Southeast Scotland. *J. Animal Ecol.* 20:33-62.
- Zar, J. H. 1974. *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, New Jersey.
- Zelt, K. A. and H. F. Clifford. 1972. Assessment of net mesh size in collecting stream insects. *Freshwater Biol.* 2:259-269.

APPENDIX

Appendix I. Stepwise regression results for Log S as the dependent variable and Log A, complexity (ratings of 1 to 6) and Log J as the independent variables.

Best Single Variable

Variables Entered	$r^2$	F	P>F
Log J	0.773	149.67	0.0001

Best Two Variables

Variables Entered	$r^2$	F	P>F
Log J	0.836	185.92	0.0001
Complexity		16.45	0.0002

All Three Variables

Variables Entered	$r^2$	F	P>F
Log J	0.842	43.11	0.0001
Complexity		18.42	0.0001
Log A		1.71	0.1981

Appendix II. Coefficient of Similarity Index values among benthic communities found on rocks of similar size and complexity.  $B_0$  was calculated from presence-absence data while  $B_1$  was calculated from relative abundance data. The lower two numbers in each cell represent the lower and upper 90% confidence interval on the mean and  $n$  = the number of comparisons in each cell.

Size	SIMPLE	MODERATE	COMPLEX
SMALL	$B_1 = 0.161$ $n = 15$ 0.063 to 0.259	$B_1 = 0.152$ $n = 10$ 0.083 to 0.221	$B_1 = 0.204$ $n = 1$ ...
MEDIUM	$B_1 = 0.234$ $n = 28$ -0.019 to 0.488	$B_1 = 0.244$ $n = 15$ 0.124 to 0.364	$B_1 = 0.265$ $n = 6$ 0.153 to 0.376
LARGE	$B_1 = 0.228$ $n = 36$ 0.120 to 0.336	$B_1 = 0.244$ $n = 1$ ...	$B_1 = 0.265$ $n = 15$ 0.217 to 0.380

Size	SIMPLE	MODERATE	COMPLEX
SMALL	$B_0 = 0.333$ $n = 15$ 0.059 to 0.607	$B_0 = 0.364$ $n = 10$ 0.198 to 0.530	$B_0 = 0.360$ $n = 1$ ...
MEDIUM	$B_0 = 0.478$ $n = 28$ 0.284 to 0.672	$B_0 = 0.489$ $n = 15$ 0.305 to 0.673	$B_0 = 0.495$ $n = 6$ 0.378 to 0.611
LARGE	$B_0 = 0.452$ $n = 36$ 0.281 to 0.623	$B_0 = 0.414$ $n = 1$ ...	$B_0 = 0.597$ $n = 15$ 0.484 to 0.709

Appendix III. Log transformed colonization curves for each COL-substrate community type.

SUBSTRATE TYPE	MODEL	F	r <sup>2</sup>	N
SMALL-SIMPLE	Log Taxa Number = 0.92(Log Day) - 0.45	67.20	0.80	20
MEDIUM-SIMPLE	Log Taxa Number = 0.77(Log Day) + 0.14	57.37	0.77	19
MEDIUM-COMPLEX	Log Taxa Number = 0.77(Log Day) + 0.21	105.58	0.86	19
LARGE-SIMPLE	Log Taxa Number = 0.81(Log Day) + 0.26	146.03	0.91	17

Appendix IV. Comparison of taxa numbers (S) between naturally occurring communities in Part I and Day 30 COL-substrate communities with the same area (90% confidence intervals included).

AREA (cm <sup>2</sup> )	ROCK COMMUNITY	SUBSTRATE COMMUNITY
31	6.72 ± 3.51	11.25 ± 1.95
274	20.93 ± 1.97	20.50 ± 0.68
1013	29.45 ± 3.97	26.67 ± 2.58

\*...S for rock areas in Part I were calculated, based on the regression line for communities on SIMPLE rocks found in Table 1.

SIMPLE Day 30 COL-substrate  
Taxa Number - Area Regression

$$\text{Log } S = 0.253(\text{Log } A) + 0.679$$

$$F = 309.11 \quad r^2 = 0.86$$

Appendix V. Average daily immigration rates calculated over each time interval (number of new taxa / Day).

(\*)...missing three days of collection, number of new taxa averaged over 6 days.

(\*\*)...missing one day of collection, number of new taxa averaged over 8 days.

(see Immigration section for explanation of missing days)

Substrate Type	Days				
	1-2	3-4	5-10	11-19	20-30
SMALL-SIMPLE #3	0.00	0.50	0.67	1.00**	0.82
SMALL-SIMPLE #4	1.00	0.50	0.50	0.33*	0.82
INTERMEDIATE-SIMPLE	1.00	1.50	0.00	1.11	0.73
INTERMEDIATE-COMPLEX	0.50	1.00	0.33	1.67	1.36
NEW MEDIUM-SIMPLE	1.00	1.00	0.33	1.00	0.53
MEDIUM-SIMPLE	1.50	1.00	0.33	1.33	1.36
NEW MEDIUM-COMPLEX	2.50	1.00	0.33	1.44	0.82
MEDIUM-COMPLEX	2.00	2.00	0.33	1.67	0.73
LARGE-SIMPLE	3.50	0.50	0.50	1.78	0.82
LARGE-COMPLEX	1.50	1.50	0.50	1.56	0.91
NATL-COMPLEX	3.00	2.50	0.70	2.00	0.89

Appendix VI. Average daily extinction rates calculated for each time interval (immigration minus colonization rate)(number of taxa / Day).

Substrate Type	Days				
	1-2	3-4	5-10	11-19	20-30
SMALL-SIMPLE	0.00	0.13	0.63	0.61	0.21
MEDIUM-SIMPLE	0.25	-0.75	0.25	0.50	0.77
MEDIUM-COMPLEX	0.75	0.50	-0.05	0.15	0.17
LARGE-SIMPLE	1.88	-1.00	-0.42	0.42	0.58

**The two page vita has been  
removed from the scanned  
document. Page 1 of 2**

**The two page vita has been  
removed from the scanned  
document. Page 2 of 2**

THE EFFECTS OF AREA AND SURFACE COMPLEXITY  
ON THE  
STRUCTURE AND FORMATION OF STREAM BENTHIC COMMUNITIES

by

William J. Trush, Jr.

(ABSTRACT)

Rocks, situated in a stream riffle, can be interpreted as islands. A sampling of macroinvertebrate communities found on a series of rocks 31 to 1000 cm<sup>2</sup> in surface area, produced a Log species- Log area curve with a slope of 0.352. This slope could not be compared to Preston's prediction of a slope value of 0.17 or 0.27 because individuals in invertebrate communities on rocks are not lognormally distributed nor are densities of individuals (per cm<sup>2</sup>) constant with area. The physical topography of the rock surface affected species numbers. Rocks with a complex surface (having crevices, smooth areas, pores, etc.) supported more taxa than rocks with simpler (mainly smooth areas) surfaces; Log species- Log area curves were steeper for a series of simple rock communities. Most taxa were not restricted to specific rock sizes or complexities, though both factors did affect population sizes.

The dynamics of stream rock invertebrate community formation was examined as were the effects of area and complexity on formation. Larger and more complex substrates had higher colonization, immigration, invasion, and replacement rates during the first 30 days of col-

onization than smaller substrates. Extinction rate was independent of substrate area (assuming constant turnover). A simulation of colonization, using random immigration and extinction, produced a colonization curve that was very similar to the actual colonization curve, though relative abundances of most taxa were altered. It was hypothesized that stream invertebrate communities are a product of random immigration and of a combination of random and deterministic extinction. Methods for monitoring the activities of individuals are needed to estimate turnover; only by assessing turnover can the importance of extinction be determined.

•