

Colonization of Natural Substrates by Stream Benthos

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Natural substrates in mesh cages in a Tompkins County, New York, woodland stream were colonized by benthic invertebrates for periods of 3, 6, 9, 12, 18, 24, 30, and 42 d during autumn 1980. An experiment was designed for the purpose of distinguishing seasonal phenology from site-specific temporal (nonseasonal) succession of colonizers. Subsequent to initial colonization, patterns of species dominance were analyzed to develop hypotheses on the potential for biological interactions as explanations for observed patterns of species succession. Total benthos and species richness increased significantly with duration of exposure of experimental substrates indicating the occurrence of nonseasonal succession. However, seasonal fluctuations in abiotic variables (water temperature, current, and water depth) were also shown to have significant effects on colonization. Colonization patterns were species specific; although most species showed gradual increases in numbers given longer exposure of substrates, some showed peak densities within the first few or after intermediate sampling periods, suggestive of competitive displacement of early by later colonists. Association analysis was conducted on the abundances of 19 species pairs within four functional feeding groups to determine the degree of co-occurrence in cages or concordance of colonization patterns. Negative associations were notably absent, and positive associations were common, especially among the filter-feeders and shredders. Positive associations could be interpreted as evidence for lack of ecological divergence (no competition), or potential for present competition. This study documents the existence of site-specific temporal succession of invertebrates in a temperate woodland stream, but does not resolve the question of the importance of biological interactions in determining community changes following initial colonization. Data gathered on a smaller spatial scale would be more sensitive to detecting negative species associations.

Des substrats naturels en cages-filets ont été colonisés par des invertébrés benthiques pendant 3, 6, 9, 12, 18, 24, 30 et 42 jours au cours de l'automne 1980 dans un cours d'eau traversant une région boisée du comté de Tompkins (New York). On a conçu un plan expérimental en vue de distinguer la phénologie saisonnière de la succession temporelle liée au site (non saisonnière) des colonisateurs. Après la colonisation initiale, on a analysé les types de dominance des espèces pour formuler des hypothèses quant à la possibilité d'interactions biologiques expliquant la succession des espèces observées. La richesse totale en benthos et en espèces s'est accrue de façon importante avec la durée d'exposition des substrats expérimentaux, ce qui indique l'existence d'une succession non saisonnière. Toutefois, on a aussi montré que les fluctuations saisonnières de variables abiotiques (température de l'eau, courant, profondeur de l'eau) avaient des effets importants sur la colonisation. Les tendances de la colonisation étaient spécifiques des espèces; bien que pour la plupart des espèces le nombre d'individus ait augmenté graduellement en fonction de la durée d'exposition des substrats, pour certaines espèces, des pics de densité étaient atteints au cours des premières périodes d'échantillonnage ou après les périodes d'échantillonnage intermédiaires, ce qui indiquerait un déplacement, par le biais de la compétition des premiers colonisateurs par les colonisateurs suivants. On a effectué une analyse des associations en étudiant l'abondance de 19 paires d'espèces, appartenant à quatre groupes d'organismes distincts d'après le mode de nutrition, pour déterminer le degré de cooccurrence dans les cages ou de concordance du mode de colonisation. On a remarqué l'absence d'associations négatives et la présence courante d'associations positives, en particulier chez les organismes filtreurs et déchiqueteurs. Les associations positives peuvent être interprétées comme l'indice d'une absence de divergence écologique (absence de compétition) ou la capacité de soutenir la compétition actuelle. La présente étude démontre l'existence d'une succession temporelle, liée au site, chez les invertébrés dans un cours d'eau traversant une région boisée tempérée, mais ne permet pas de déterminer le rôle que jouent les interactions biologiques dans les changements qui surviennent dans la communauté après la colonisation initiale. Des données prélevées sur une échelle spatiale plus petite permettraient de déceler de façon plus sensible les associations négatives d'espèces.

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The processes of colonization and subsequent changes in dominance of species (succession) are common in streams subject to seasonal and unpredictable disturbances, such as floods and scouring (Sousa 1984). The world of riffle-dwelling aquatic invertebrates has been recently characterized by Sheldon (1984, p. 401) as "an everchanging mosaic of environments in which elements arise, vanish, and

reappear with different periodicities and predictabilities." This description illustrates the importance of colonization (defined as the process by which individuals or groups of individuals become established in habitats) in the life cycles of stream invertebrates. Another recent review by Fisher (1983) suggests that stream ecologists know little about the process of site-specific temporal succession by macrobenthos.

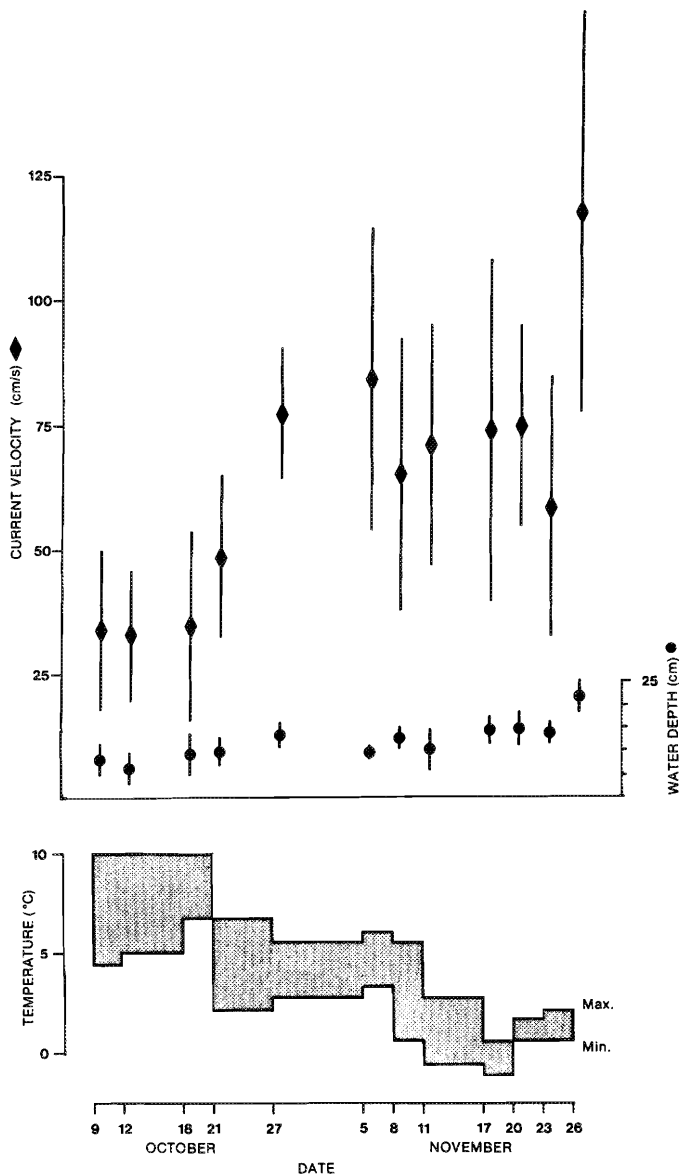


FIG. 1. Environmental variables over the sampling period: mean \pm 2 SE current velocity, water depth, and maximum–minimum temperatures.

The severity and frequency of disturbances determines the degree of population depression (whether colonization is necessary) and the nature of the subsequent adjustments in species dominance (Hemphill and Cooper 1983). The factors influencing colonization and succession may be allogenic (external, abiotic), or autogenic (internal, biotic); autogenic succession may be interactive, where present communities influence establishment of future communities, or noninteractive, a simple function of such factors as species life histories (see Fisher 1983 and Sheldon 1984 for more detailed discussion). Fisher (1983) suggested that where disturbances are frequent (for example, weekly spates of heterotrophic New England streams), succession might not be expected to occur. In sharp contrast, streams that flood annually, such as the Sonoran Desert stream studied by Fisher et al. (1982), have sufficient time for species readjustments and may show marked successional patterns.

The frequency and severity of disturbance also affects the temporal and spatial scales of colonization events (Sheldon 1984) and available source of colonizers or the "colonization

pool" for reestablishment of communities in the affected portion of streams (Gore 1982). If the disturbance is catastrophic, affecting a large area of stream, succession will be slower than in situations where disturbances are of a smaller magnitude (Minshall et al. 1983). In fact, many stream communities can probably tolerate periodic disturbances and do not change with frequent disturbance but adjust through periodic fluctuations in existing populations (Clifford 1982; Fisher 1983).

The purpose of this study was to examine the colonization and subsequent patterns of species dominance on natural stream substrates confined to enclosures in a temperate woodland stream in the Finger Lakes region of New York. The data provide a test of Fisher's (1983) hypothesis that site-specific temporal succession should not occur, since the test stream is a typical heterotrophic New England stream. The temporal scale of colonization was relatively short (7 wk) and spatial scale small (microlevel: 10 cm – 10 m, Sheldon 1984). Temporal patterns of change in total numbers of individuals, species richness, and of densities of dominant species were examined. Data were also examined for temporal and spatial overlap of closely related species to develop hypotheses on the potential for biological interactions, such as competition, as explanations for observed patterns of species succession.

Materials and Methods

Experiments were carried out in upper Six Mile Creek, a third-order stream flowing through the Slaterville Wildflower Preserve in Tompkins County, New York. The stream has a riparian zone with dense deciduous vegetation providing a rich allochthonous input typical of heterotrophic New England streams. The substrate is a Devonian shale and siltstone with heterogeneous particle sizes ranging from flat stones of over 1 m in diameter to underlying gravel and silt. Discharge fluctuates with frequent rain storms during most of the year and with periodic freeze–thaw and snowmelt during the winter. Since the stream drains a large watershed (12 800 ha) with poorly drained soils, it is particularly sensitive to rainfall (Bukantis 1983). The study site was a 40-m riffle section of stream with heterogeneous cobble substrate bounded by a pool upstream and terraced bedrock slabs downstream. Abiotic conditions (current velocity, water depth, and water temperatures) over the experimental period are shown in Fig. 1. No major flooding occurred during this period.

Enclosures (stainless steel screen, mesh = 800 μ m, dimensions 30 \times 20 \times 10 cm, see Peckarsky 1984) were filled with natural stream substrate standardized for number and size of particles (20 particles: with largest diameters of <5 (9), <10 (6), <15 (3), and <20 cm (2)). Each stone was carefully washed in stream water to remove all invertebrates while minimizing the disturbance of natural periphyton assemblages. Cages were placed in the stream bottom essentially flush with the surface of the substrate (covered with a thin layer of stones (5 cm) to prevent vandalism) for periods of 3, 6, 9, 12, 18, 24, 30, and 42 d from 9 October to 26 November 1980. The time period for the experiment was in the range of that of other studies in which the substrates to be colonized were immediately adjacent to the pool of invertebrates available for colonization (Ulfstrand et al. 1974; Allan 1975; Sheldon 1977; Williams 1977; Wise and Molles 1979; Shaw and Minshall 1980; Hemphill and Cooper 1983). Mesh baffles (10 \times 30 cm) with 1-cm openings were placed on upstream and downstream ends of the cages to allow migration of benthos from two directions. Since seasonal changes are known to affect colo-

TABLE 1. Summary of the experimental design. Numbers denote date of retrieval of two cages for each treatment, except when otherwise noted in parentheses.

Treatment (days in Stream)	Dates retrieved (day 0 = Oct. 9, day 48 = Nov. 26)
3	3 (4 cages), 33, 42, 45, 48 (4 cages)
6	9, 18, 48
9	9, 12, 42
12	12, 39, 45
18	18, 30, 48
24	27, 33, 42
30	30, 39, 48
42	42 (4 cages), 45

nization of stream substrates by benthic invertebrates (Williams 1980; Hemphill and Cooper 1983; Ciborowski and Clifford 1984), the experiment was designed such that, wherever possible, the six replicates per treatment (time in stream) were staggered seasonally with two cages per treatment buried and retrieved in each of early, middle, and late autumn (Table 1). This design was somewhat restricted by the number of cages available (20) and the practicality of field work during late autumn in central New York (Fig. 1). However, date retrieved (season) was not correlated with days in stream (duration of exposure) per cage ($r_s = 0.135$, $N = 56$); therefore, the experimental design allows effective separation of site-specific temporal succession from seasonal succession.

On days when cages were buried and retrieved, water depth and current velocity were measured at the surface of each cage, and water temperature was monitored throughout the experimental period with a maximum–minimum thermometer. Sites for cage placement were chosen to minimize spatial variability in these physical factors.

Results

Abundance of Total Benthos

Number of macroinvertebrates per cage generally increased with duration of the experimental period (Fig. 2). These data do not include very small instars or species in the benthos, since these forms were not retained by the cage mesh (800 μm) designed to minimize interstitial flow reduction. Numerical data were log-transformed to stabilize variance and subjected to a two-way ANOVA to test for effects of duration of exposure of cages to colonization (number of days) and season (date retrieved) on the resultant colonization (total number of individuals per cage). The results, given in Table 2, show a highly significant effect of number of days on colonization with a nearly significant ($p = 0.0577$) effect of season, and no significant interaction between duration of exposure and date retrieved. These data suggest that the total number of colonists per cage is strongly affected by length of time the cage remains in the stream, with a lesser, but probably important, seasonal effect. Since “replicate” cages for each treatment (duration) were exposed during different times of the season (Table 1), this seasonal effect could explain in part the larger error bars shown in Fig. 2.

To analyze the effect of the abiotic regime on colonization of cages over the period of exposure in the stream, simple and partial correlations were performed on log-transformed numerical data with duration of colonization period and abiotic vari-

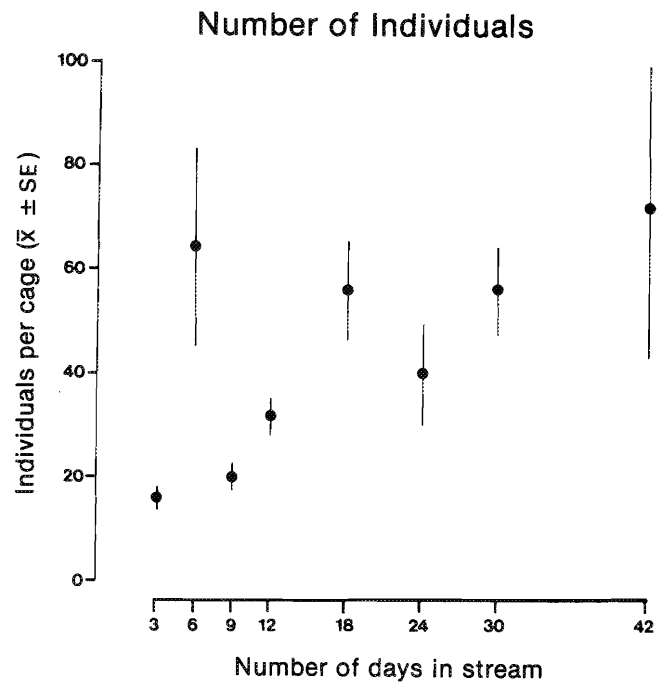


FIG. 2. Mean total number of individuals colonizing cages left in the stream for 3–42d.

TABLE 2. Results of two-way ANOVA on log-transformed data for total number of individuals and total number of species versus duration of exposure of substrates to colonization (days in stream) and season (date retrieved) (* = significant, ns = not significant).

	F	p	Significance
<i>Individuals: F = 4.48, p < 0.0001</i>			
No. of days	6.66	0.0001	*
Date retrieved	2.08	0.0577	ns
Interaction	0.47	0.8521	ns
<i>Species: F = 2.89, p < 0.003</i>			
No. of days	3.76	0.0046	*
Date retrieved	0.93	0.5213	ns
Interaction	0.65	0.7097	ns

ables. Log number of colonists was positively correlated with the duration of the colonization period (Table 3). There were no simple correlations between numbers of colonists and any physical variables measured on the placement or retrieval date. Therefore, colonization patterns did not simply reflect abiotic conditions on the cage placement or removal date. However, number of colonizers were significantly associated with the changes in the abiotic regime over the period of each cage's exposure in the stream. The log of the numbers of colonists per cage was significantly correlated with the change in current velocity, change in depth, and the change in temperature that occurred during the specific period over which each cage was in the stream (Table 3). In other words, colonization rates were higher in cages over which flow and water depth increased and temperature decreased during their residence in the stream.

Partial correlations allowed examination of the relationship between number of colonists and colonization period, holding

TABLE 3. Summary of simple and partial correlation coefficients (r) with associated probabilities in parentheses (ns = not significant; $N = 56$).

	Days in stream	Change in flow	Change in depth	Change in temperature
<i>Simple correlations</i>				
Number of individuals	0.574 (0.001)	0.303 (0.02)	0.430 (0.001)	-0.529 (0.0001)
Number of species	0.616 (0.001)	0.224 (ns)	0.401 (0.002)	-0.518 (0.0001)
<i>Partial correlations holding colonization period constant</i>				
Number of individuals		0.243 (ns)	0.307 (0.05)	-0.047 (ns)
Number of species		0.141 (ns)	0.261 (ns)	0.087 (ns)
<i>Partial correlations holding abiotic variables constant</i>				
Number of individuals	0.148 (ns)			
Number of species	0.206 (ns)			

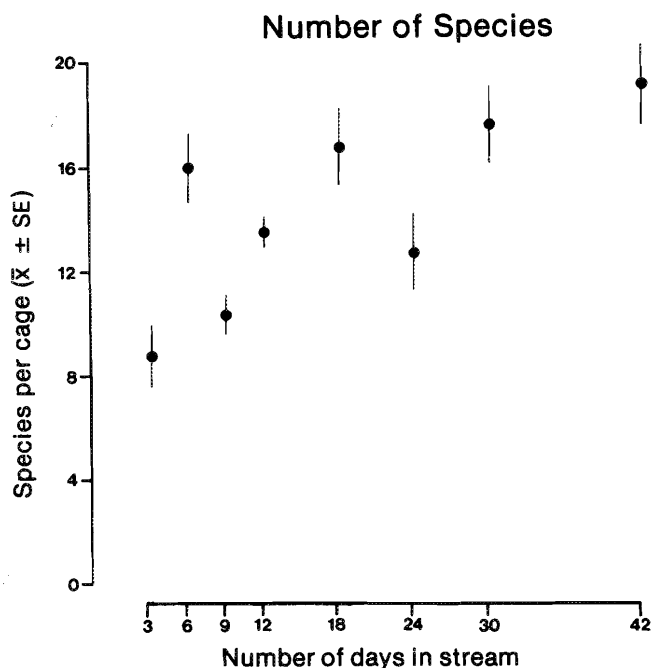


FIG. 3. Mean number of species colonizing cages left in the stream for 3–42 d.

the effects of abiotic change constant, and the relationship between colonization and abiotic change, holding effects of colonization period constant. Thus, this analysis indicates which factor (time or abiotic change) may be more important. When abiotic factors (change in flow, change in depth, and change in temperature) were held constant, the correlation between log number of colonists and colonization time was not significant (Table 3). When colonization time was held constant, the correlations between log number of colonists and abiotic factors (except change in depth) became nonsignificant. This analysis indicates that the correlation between numbers of colonists and duration of colonization period is largely a

reflection of the relationship between time and the change in abiotic regime. This experiment should be repeated under opposite conditions of abiotic change (summer: decreasing flow and depth, increasing temperature) to confirm this observation.

The 19 most abundant taxa were examined individually for associations between colonization (numbers) and date cages were retrieved from the stream to assess which species were contributing to the observed seasonal effect on total invertebrate abundance. Two taxa (*Isoperla*, *Heptagenia*) were more abundant earlier in this study ($r_s = -0.244$, -0.268 , $N = 56$), and one species (*Epeorus* sp.) appeared in greater numbers later in the study ($r_s = 0.312$, $N = 56$). The other 16 species showed no significant seasonal trend in abundance over the time period of the study.

The total number of species colonizing cages ranged from 23 to 39 summed over all cages per treatment, with 63 total species recovered during the experiment (not including detailed analysis of chironomids, which were rare in these substrates). The total number of species generally increased with time experimental substrates were in the stream. The pattern of change in species richness per cage with increasing numbers of days substrates remained in the stream was essentially the same as that of total benthic colonization (Fig. 3); greater species richness occurred with increased duration for colonization (Table 3). Species richness data were also log-transformed and subjected to a two-way ANOVA to determine the effects of duration of colonization and date retrieved on number of species recovered per cage. In this case, a highly significant effect of days in stream was obtained with no significant seasonal effect or interaction between duration and date retrieved on species colonization of cages (Table 2). This result suggests that over the time period of the experiment (9 October – 26 November) there was site-specific (nonseasonal) temporal succession in number of species, but no seasonal succession in species richness.

Species richness data were also subjected to simple and partial correlation analyses with duration of colonization period and change in abiotic variables. The results of this analysis

Shredders

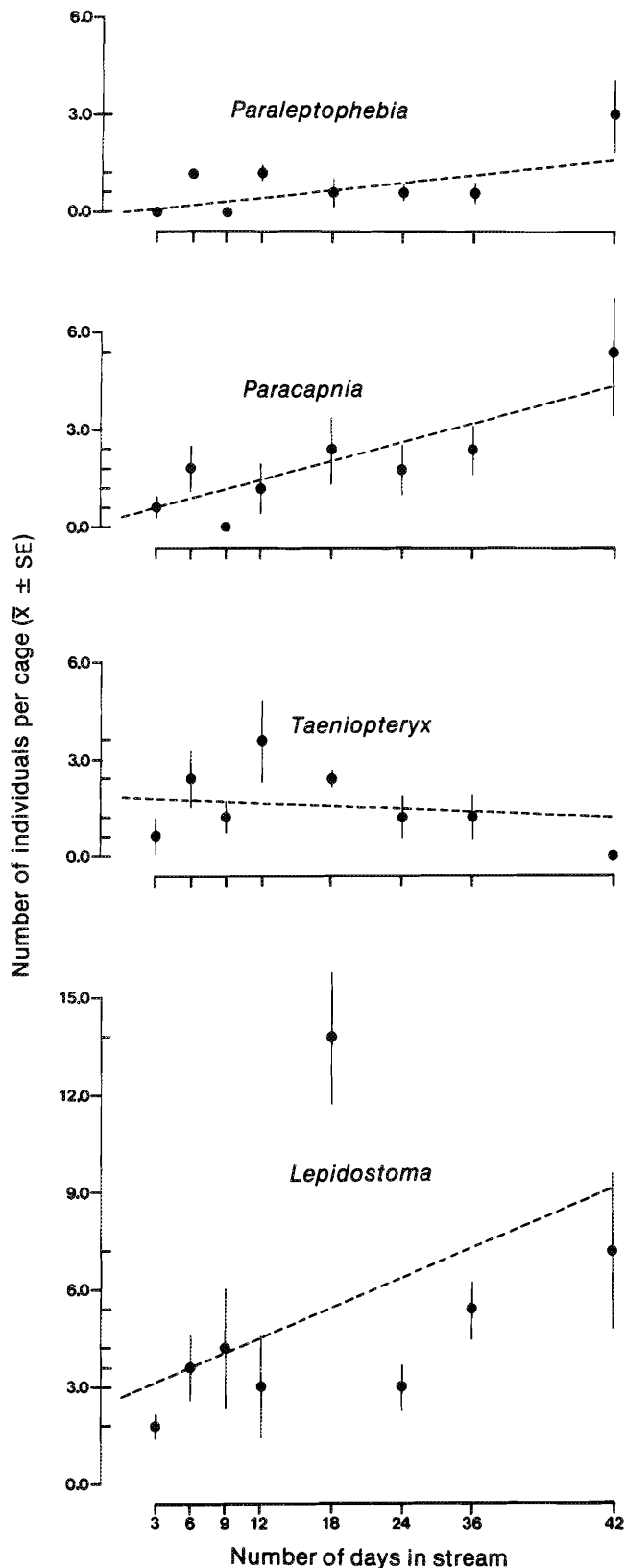


FIG. 4. Number of shredders (*Paraleptophebica*, *Paracapnia*, *Taeniopteryx*, *Lepidostoma*) colonizing cages left in the stream for 3–42 d. Broken lines are least-squares regression lines, or the hypothetical pattern of colonization if the average rate had prevailed throughout all trials.

were the same as those for total numbers of colonists (Table 3). Therefore, the trend for increased species richness given longer colonization time is largely a reflection of the relationship between change in abiotic regime and colonization time.

Patterns of Individual Taxa

Temporal (nonseasonal) patterns of colonization were examined for the 19 most abundant taxa recovered in the cages. Three questions were considered for each species: (1) Did the density of individuals increase, decrease, or show a complex pattern with respect to time allowed for colonization? (2) Did the colonization rate differ from constant over the range of time periods? (3) Did species that share resources show similar patterns of colonization?

To answer the first question, colonization data for each species were plotted separately (Fig. 4–7), and patterns were tested statistically, using Spearman rank correlation coefficients, for significant association between population density and days of colonization. Most taxa (13 of 19) showed significant increases in number per cage with increasing days in the stream (Table 4), contributing to the trend for all taxa combined (Fig. 2). One species (*Pseudocloeon* sp.) significantly decreased in abundance with increasing time for colonization (Fig. 5), and five taxa showed complex patterns of colonization with time. *Taeniopteryx*, *Baetis*, and *Isoperla* showed peak rates of colonization with 12 d of cage exposure. *Epeorus* showed a bimodal pattern with peaks occurring at 12 and 30 d; *Glossosoma* colonization resembled a normal curve, with highest numbers recovered after 18 d of cage exposure. Variation in the composite of all species combined (Fig. 2) reflects the differences in colonization patterns among individual taxa.

To answer the second question, hypothetical colonization curves were drawn on the plots of the actual data that represent least-squares regression lines assuming that the daily rate of colonization was constant for a given species, as if the average rate of colonization had prevailed throughout the treatments (Ulfstrand et al. 1974). Comparison of actual data with hypothetical curves reveals deviations from constant colonization rates. A few taxa had fairly constant, but low, rates of colonization (*Ephemera*, *Dolophilodes*). Most taxa showed increasing (*Paracapnia*, *Paraleptophebica*, *Eurylophella*, *Stenonema*, *Agnatina*, *Sweltza*) or decreasing (*Taeniopteryx*, *Lepidostoma*, *Pseudocloeon*, *Baetis*, *Glossosoma*, *Cheumatopsyche*, *Hydropsyche*, *Acroneuria*, *Isoperla*) colonization rates given longer cage exposure in the stream. The 42-d treatment contributed the most deviation from the regression line for those taxa with increasing-rate patterns. Those with decreasing-rate patterns showed a variety of peaks, from 6 to 30 d (Fig. 4–7).

Visual comparison of the colonization patterns by functional feeding categories (those species sharing common resources) suggests that differences occur in some cases, but not others. Taxa were classified into feeding groups based on detailed behavioral and morphological data and stomach contents in some cases (e.g. *Acroneuria* and *Agnatina*, Peckarsky and Penton 1985) and on information from the literature in other cases (Merritt and Cummins 1984). Statistical analysis of similarities in colonization patterns of taxa within feeding groups was conducted to examine the potential influence of biological interactions (such as competition) on species successional patterns (Sheldon 1984). Abundances of species pairs per

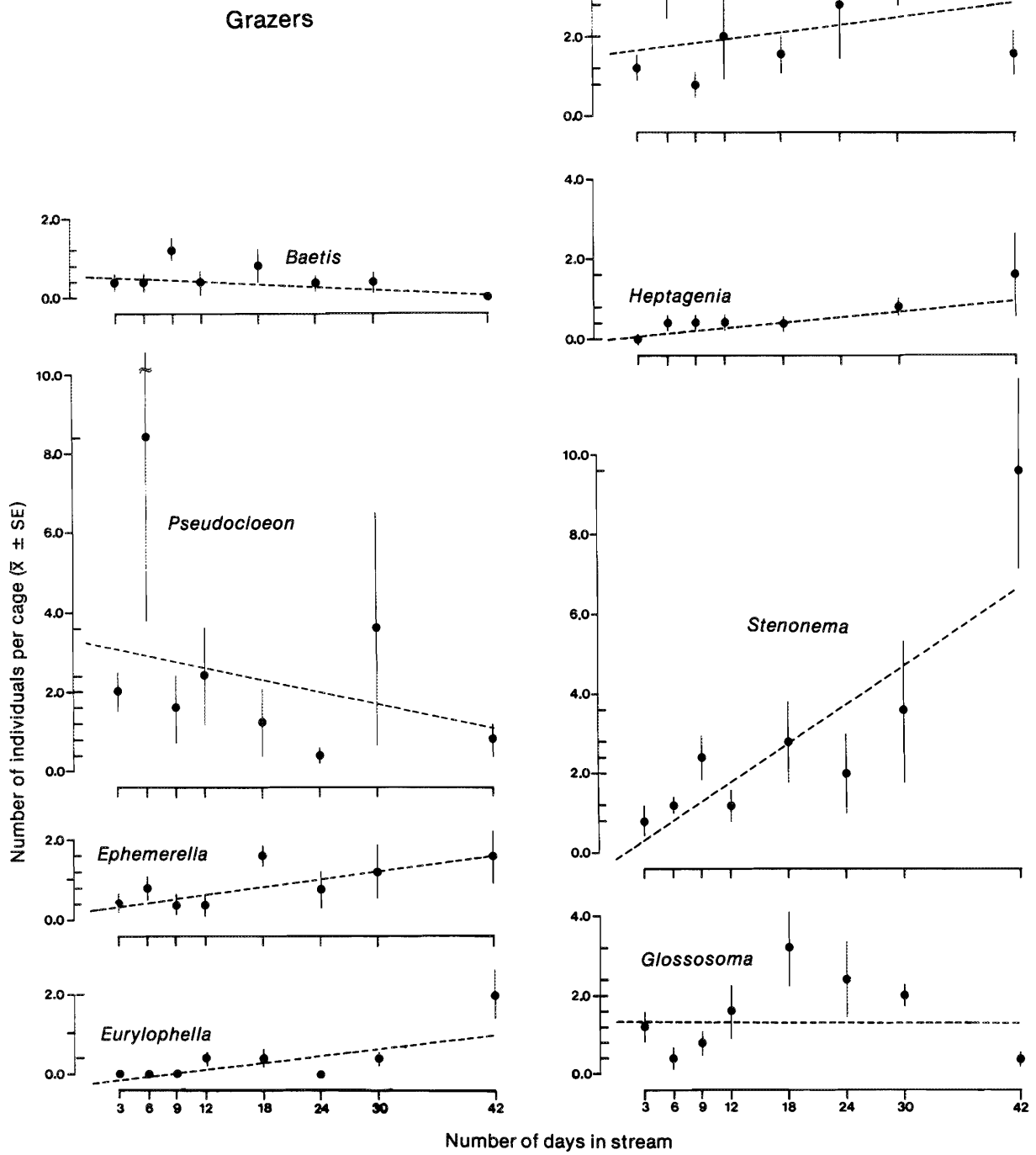


FIG. 5. Number of grazer/collectors (*Baetis*, *Pseudocloeon*, *Ephemera*, *Eurylophella*, *Epeorus*, *Heptagenia*, *Stenonema*, *Glossosoma*) colonizing cages left in the stream for 3–42 d. Broken lines are least-squares regression lines, or the hypothetical pattern of colonization if the average rate had prevailed throughout all trials.

age were compared using Spearman rank correlation coefficients to determine whether significant positive or negative associations occurred between species sharing common resources. This analysis is more sensitive than presence/absence indices (Pielou 1977), since relationships are expressed as a gradient of abundances. Competition often reduces densi-

ties but does not always result in exclusion of inferior species (Hart 1983).

The most striking feature of this analysis is a lack of significant negative associations (Table 5). Only one species pair (*Baetis* and *Eurylophella*) of 43 comparisons showed a negative correlation in abundances per cage; this result is well below

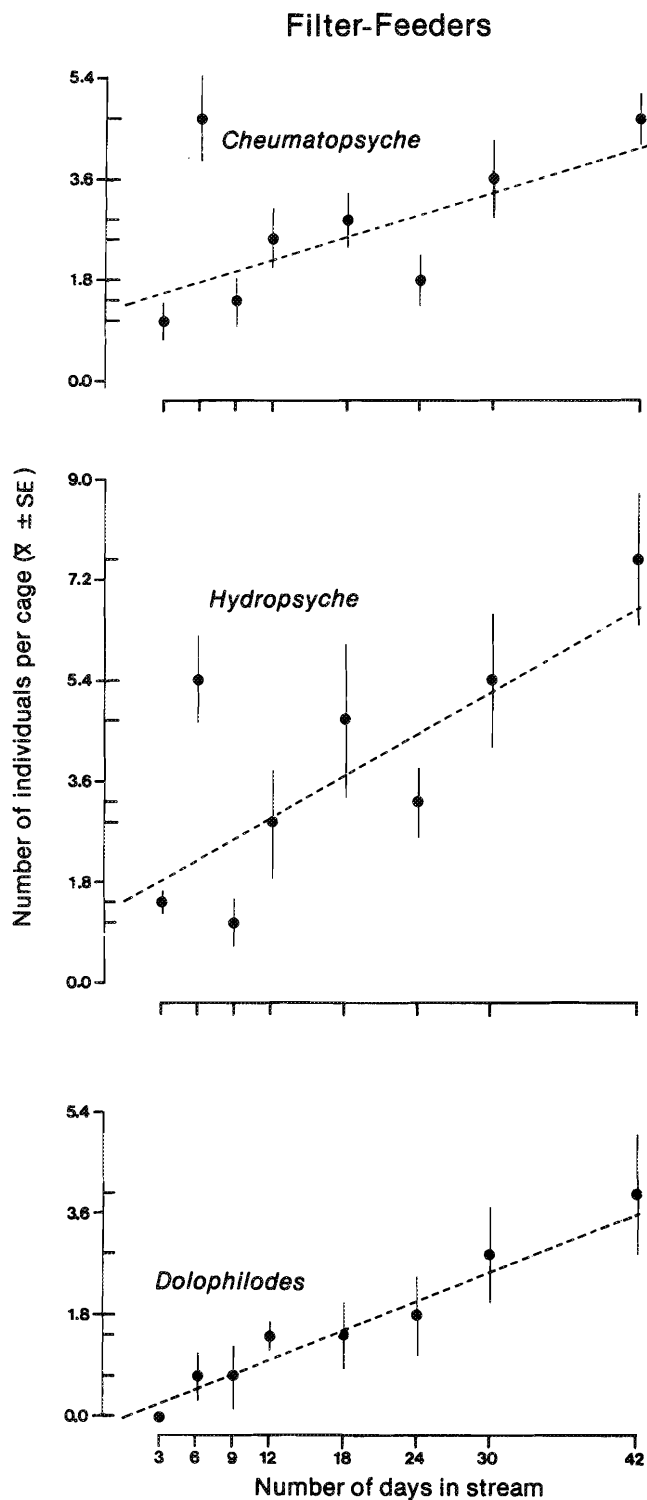


FIG. 6. Number of filter-feeders (*Cheumatopsyche*, *Hydropsyche*, *Dolophilodes*) colonizing cages left in the stream for 3–42 d. Broken lines are least-squares regression lines, or the hypothetical pattern of colonization if the average rate had prevailed throughout all trials.

the 5% level for significant results due to chance alone. On the other hand, a large number of positive associations occurred among species within functional feeding groups, especially among the filter-feeders (all of which were positively associated) and shredders (two thirds of which were positively corre-

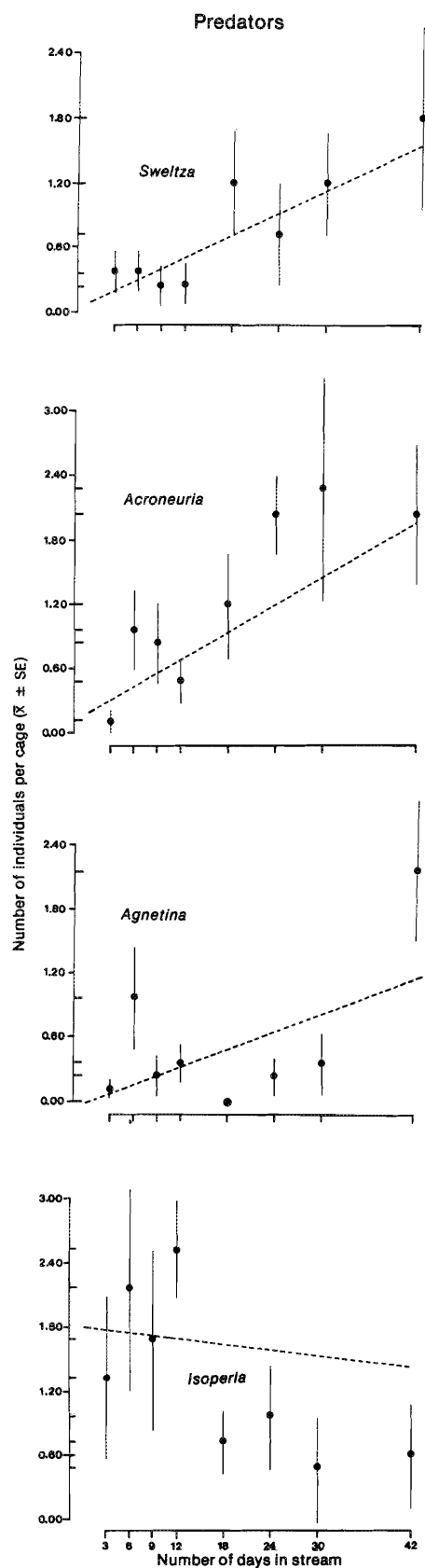


FIG. 7. Number of predators (*Sweltza*, *Acroneuria*, *Agnetina*, *Isoperla*) colonizing cages left in the stream for 3–42 d. Broken lines are least-squares regression lines, or the hypothetical pattern of colonization if the average rate had prevailed throughout all trials.

TABLE 4. Summary of results of Spearman rank correlation analysis on numbers of individuals per cage versus days in stream for 19 abundant taxa.

Functional feeding groups	Increased in number with days in stream	Decreased in number with days in stream	Complex pattern with days in stream
Shredders	<i>Paraleptophlebia</i> <i>Paracapnia</i> <i>Lepidostoma</i>	None	<i>Taeniopteryx</i>
Grazer/collectors	<i>Ephemera</i> <i>Eurylophella</i> <i>Heptagenia</i> <i>Stenonema</i>	<i>Pseudocloeon</i>	<i>Baetis</i> <i>Epeorus</i> <i>Glossosoma</i>
Filter-feeders	<i>Cheumatopsyche</i> <i>Hydropsyche</i> <i>Dolophilodes</i>	None	None
Predators	<i>Acroneuria</i> <i>Agnatina</i> <i>Sweltza</i>	None	<i>Isoperla</i>

TABLE 5. Summary of the species associations among members of the same functional feeding group. Significant correlation coefficients (r_s) are given and noted with asterisks ($N = 56$; ns = not significant).

	<i>Paralep.</i>	<i>Paracap.</i>	<i>Taeniop.</i>	<i>Lepidos.</i>				
Shredders								
<i>Paraleptophlebia</i>	—	(0.403)*	ns	ns				
<i>Paracapnia</i>		—	(0.283)*	(0.304)*				
<i>Taeniopteryx</i>			—	(0.388)*				
<i>Lepidostoma</i>				—				
	<i>Baet.</i>	<i>Pseu.</i>	<i>Ephe.</i>	<i>Eury.</i>	<i>Epeo.</i>	<i>Hept.</i>	<i>Sten.</i>	<i>Glos.</i>
Grazer/collectors								
<i>Baetis</i>	—	(0.340)*	ns	(-0.227)*	ns	ns	ns	ns
<i>Pseudocloeon</i>		—	ns	ns	(0.282)*	ns	ns	ns
<i>Ephemera</i>			—	(0.348)*	(0.476)*	(0.235)*	(0.332)*	ns
<i>Eurylophella</i>				—	ns	ns	(0.408)*	ns
<i>Epeorus</i>					—	ns	ns	ns
<i>Heptagenia</i>						—	ns	ns
<i>Stenonema</i>							—	ns
<i>Glossosoma</i>								—
	<i>Cheuma.</i>		<i>Hydrop.</i>		<i>Doloph.</i>			
Filter-feeders								
<i>Cheumatopsyche</i>		—		(0.622)*		(0.549)*		
<i>Hydropsyche</i>				—		(0.493)*		
<i>Dolophilodes</i>						—		
	<i>Acron.</i>	<i>Agnat.</i>	<i>Swelt.</i>	<i>Isope.</i>				
Predators								
<i>Acroneuria</i>	—	(0.247)*	ns	ns				
<i>Agnatina</i>		—	ns	ns				
<i>Sweltza</i>			—	ns				
<i>Isoperla</i>				—				

lated). These data indicate that shredders and filter-feeders tend to overlap in their distributions among cages, and show striking similar colonization patterns. Seven of 28 comparisons among grazer/collector species (one fourth) showed significant positive association, suggesting moderate overlap among

taxa within this functional group. The feeding group with the fewest associations was the predators, with only the two large perlid species, *Acroneuria carolinensis* and *Agnatina* (formerly *Phasganophora*) *capitata*, showing positive correlations between numbers per cage.

Discussion

Increases in abundance of the total benthos with increasing exposure of experimental substrates to colonization were consistent with those observed by other investigators (Allan 1975; Wise and Molles 1979; Shaw and Minshall 1980; Fisher et al. 1982; Minshall et al. 1983; Ciborowski and Clifford 1984). Species richness did not increase and then decrease to moderate levels over time as in Siegfried and Knight (1977) and Gore (1982), but showed the same pattern as that of total numbers as in Allan (1975), Minshall et al. (1983), and Wise and Molles (1979). This could be due to the dependency of this variable on sample size (Peet 1974), or suggestive that biological interactions were not influencing species succession (Sheldon 1984). These data do not allow determination of mechanism.

The unique aspect of this study is the separate examination of site-specific temporal succession (effect of duration of cage exposure independent of season) and seasonal succession (effect of date of cage retrieval) and interactions between these variables (by two-way ANOVA). The results are strongly supportive of the existence of site-specific temporal succession and no seasonal succession of species richness over the period of the experiments. These results are in conflict with the suggestion made by Fisher (1983) that nonseasonal, temporal succession should be rare in New England deciduous forest streams such as Six Mile Creek, subject to frequent flooding disturbances. However, no severe storms or flooding events occurred during the experiment (Fig. 1). Results of the analysis of total numbers of individuals are less clear; significant temporal succession did occur, but a nearly significant seasonal effect on accumulation of individuals in cages was also shown. Three taxa that became either more or less abundant over time (*Isoperla*, *Epeorus*, *Heptagenia*) probably contributed to this effect. However, since 16 of 19 species analyzed showed no significant seasonal change in numbers over the experimental period, and the duration of cage exposure to colonization was shown to be independent of season (date retrieved), the data argue convincingly for a greater relative importance of site-specific temporal succession.

Neither patterns of total abundance nor species richness appeared to approach an asymptote with rates of increase clearly declining over duration of exposure of substrates (Fig. 2 and 3). The time required for stabilization of numbers cannot be clearly determined due to large variation in the data. One might speculate that stabilization time was less than that of Minshall et al. (1983) (439 d) but greater than that measured by Wise and Molles (1979) (9 d), and comparable with that estimated by Townsend and Hildrew (1976) (37.5 d). These broad differences were probably due to the proximity of the available colonization pool of benthic invertebrates, as well as the time of year during which experiments were conducted. The stream under investigation by Minshall et al. (1983) was catastrophically disturbed by the breaking of a dam and release of torrential flood waters, followed by artificial man-made diversion for channel and bridge repair. Thus, the affected area was very large and colonization pool relatively remote. Wise and Molles (1979) conducted their study in a different geographical area during April, a season in which Williams (1980) found higher colonization levels than during the October–November period studied here. Alternatively, the New Mexico stream may be more characteristic of autotrophic streams

suggested by Fisher (1983) to show rapid recovery from disturbances.

The patterns I observed could best be described as redistribution of the benthos in response to availability of newly opened habitats (Townsend and Hildrew 1976) rather than succession following catastrophic scouring events (Minshall et al. 1983). In Six Mile Creek, habitats probably become available through local disturbance of sediments during periodic spates, as in McAuliffe (1983). The experiment reported here simulated this situation with artificial removal of all invertebrates from substrate patches and observation of the responses of the benthos. However, periphyton and associated aufwuchs were not removed, leaving a food source for potential colonists, and providing thereby a favorable substrate patch (Sheldon 1984).

The partial correlation analysis of numbers of invertebrates colonizing cages with changes in depth, current velocity, and temperature over the period of exposure of the substrates suggest a possible response by benthos to changes in abiotic conditions. These data corroborate the conclusion of Ciborowski and Clifford (1984) that the influence of current regime is of primary importance in determining the rate and pattern of benthic colonization. These studies do not allow a determination of the mechanism for this effect, which could be that current either stimulates active migration or causes passive transport of animals.

Examination of patterns of colonization of individual species corroborates findings of previous studies that rates of colonization are species specific. For example, baetids have been identified as early colonizers or opportunistic taxa in Colorado (Allan 1975), Sweden (Ulfstrand et al. 1974), Arizona (Fisher et al. 1982), Montana (McAuliffe 1983), Idaho (Minshall et al. 1983; Shaw and Minshall 1980), and Alberta (Ciborowski and Clifford 1984) streams. Here, one other grazer (*Glossosoma*), one shredder (*Taeniopteryx*), and one predator (*Isoperla*) also increased, and then decreased in density with time of exposure of experimental substrates. One grazer (*Epeorus*) showed a bimodal pattern of colonization. These patterns are consistent with the hypothesis that biological interactions may influence alterations in species dominance in the benthic community as a whole (Sheldon 1984). Potentially, the "pioneer" species may be replaced by superior competitors that are slower colonizers, as in Hemphill and Cooper (1983). Possible candidates are shown in Table 4 (other grazing mayflies displacing baetids and *Glossosoma*, other predaceous stoneflies replacing *Isoperla*, and other shredding species replacing *Taeniopteryx*). However, lack of significant negative associations between these species on an individual cage basis casts doubt on this interpretation (Table 5). On the scale of one unit of colonization (a cage), these data provide no support for the existence of a negative interaction between species. If such interactions are producing the whole community pattern shown in Fig. 4, 5, and 7, they must be occurring at a scale smaller or larger than that of the cages.

The association analysis only allows formulation of hypotheses concerning the potential of biological processes, such as competition, for controlling the community changes subsequent to initial colonization. Although confamilial benthic insects often share behavioral and morphological characters that make them likely candidates for competitive interactions, species that are not closely related phylogenetically but share common resources are also subject to potential competition (Hart 1983). The lack of negative association between potential

competitor species as in Reice (1981, 1983) has been interpreted as lack of evidence for competition. However, as discussed in Reice (1981), these analyses are not definitive; for example, positive associations among the coexisting shredders, filter-feeders, grazers, and predators could be attributed to any of the following hypotheses. Both species of each pair could be responding to the same environmental parameter(s) or availability of favorable habitats resulting in the observed significant overlap. The species pair may not competitively interact; or the species pair could be in present competition, not intense enough to have driven species to evolve separate distributions. Direct experimental evidence is needed to test these alternative hypotheses to explain significant associations. For example, behavioral experiments have shown that the two perlid species (*Acronuria* and *Agetina*) exhibit interference competition (Peckarsky and Penton 1985) and that related hydropsychid species aggressively defend catch-nets from intrusion by con-familial competitors (Jansson and Vuoristo 1979). Alternatively, the scale of the experiment described here might be too large to detect negative associations such as those demonstrated on a smaller scale for grazers in a Montana stream (McAuliffe 1984).

The data from this experiment support the following conclusions. Significant site-specific temporal succession in accumulation of total benthic invertebrates and numbers of species occurred in Six Mile Creek over the period of 9 October – 26 November 1980. A secondary seasonal successional effect was also observed for total abundances, primarily affecting 3 of 19 species tested, but not for species richness. Patterns of colonization were species specific with 13 taxa gradually increasing, 1 species decreasing in numbers, and 6 species showing more complex changes over the range of duration of exposure of cages to colonization. Those with complex colonization patterns generally showed peak abundances after intermediate lengths of cage exposure. Many pairs of filter-feeders, shredders, and to a lesser extent grazers and predators showed significant positive associations in numbers per cage. These data are suggestive but insufficient for drawing rigorous conclusions regarding the importance of biological interactions in governing community changes subsequent to initial colonization.

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