

Short-Term Colonization Patterns of Lotic Macroinvertebrates

Jan J. H. Ciborowski¹ and Hugh F. Clifford

Department of Zoology, University of Alberta, Edmonton, Alta. T6G 2E9

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To establish colonization of gravel-filled trays by aquatic invertebrates, we used concurrent simultaneous placement/sequential removal and sequential placement/simultaneous removal sampling schedules over 12-d intervals in a river of central Alberta. Colonization trays collected more taxa and greater numbers of animals than did unit area (Hess) samples of the natural substrate. There was no correlation between rank of abundance of the 10 most prevalent taxa found in colonization trays and in Hess samples. The two sampling schedules produced significantly different estimates of colonization rate and numbers for 6 of 10 abundant taxa. From hypothetical colonization curves derived for *Baetis tricaudatus* Dodds larvae from information on drift tendencies and settling abilities, we suggest that temporal pattern of tray colonization is strongly dependent on fluctuations in mean current velocity and short-term changes in upstream benthic density.

Pour estimer la colonisation de plateaux de graviers par les invertébrés aquatiques, nous avons utilisé des calendriers d'échantillonnage, se répétant tous les 12 jours, prévoyant d'une part le placement simultané suivi de retrait séquentiel ou, d'autre part, le placement séquentiel suivi de retrait simultané. Les essais ont été effectués dans une rivière du centre de l'Alberta. Le nombre d'espèces dans les plateaux était supérieur au nombre trouvé dans les échantillons (de Hess) des substrats naturels. Il n'y avait pas de corrélation entre le rang d'abondance, pour les 10 espèces les plus nombreuses, dans les plateaux de colonisation et les échantillons de Hess. Les deux modes d'échantillonnage conduisaient à des estimations différant de façon significative des taux de colonisation et des nombres d'individus pour 6 des 10 espèces les plus abondantes. Des courbes hypothétiques de colonisation obtenues pour les larves de *Baetis tricaudatus* Dodds à partir de données sur la dérive et l'aptitude à se déposer laissent à penser que la colonisation des plateaux en fonction du temps dépend fortement des variations de vitesse du courant et des modifications à court terme de la densité benthique en amont.

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Colonization studies have become an increasingly popular means of examining the composition of lotic communities. Sample substrates can be standardized, thus reducing intersample variability and permitting controlled tests of factors that might influence the benthic community (Rabeni and Minshall 1977; Culp et al. 1983). Colonization methods are particularly valuable in large rivers where standard benthic sampling is difficult. However, artificial substrates only approximate natural river substrate and do not always collect a sample representative of the benthic community. Because individuals of different taxa colonize at different rates, it is often unclear how long artificial substrates must remain in place before they become representative. Rosenberg and Resh (1982) comprehensively reviewed the benefits and shortcomings of artificial substrate methodology.

Traditionally, colonization studies have followed a "simultaneous placement" (SP) design; all samplers are introduced at one time and are subsequently recovered according to some predetermined schedule (Ulfstrand et al. 1974; Rabeni and Minshall 1977). This technique is appropriate for monitoring seasonal changes in species composition or abundance. How-

ever, where the colonization process itself is of interest (e.g. a comparison of colonization among treatments) a more suitable design is "simultaneous removal" (SR) (Shaw and Minshall 1980). By this method, samplers are periodically set in place and all are removed on the last day of the study. This ensures that all samplers are exposed to similar fluctuations in environmental conditions, at least immediately prior to recovery, and that animals collected are from the same sampling population. A shortcoming of this method is that stream perturbations can result in loss of all samples. Sheldon (1977) suggested that this problem might be minimized by estimating colonization rate and/or extrapolating equilibrium numbers of individual taxa from data collected over relatively short intervals.

Luttrell and Meier (1982) compared SP and SR designs over 12 wk and found substantial differences in accumulation of periphyton chlorophyll *a*, macroinvertebrate abundance, and standing biomass. Our study evaluates short-term colonization trends of individual taxa and examines the applicability of Sheldon's (1977) methods. Our specific objectives were to determine whether (1) colonization trays exposed for short periods collect a representative sample of the local benthic community, (2) SP and SR sample schedules reflect the colonization process equally well, and (3) the colonization process is significantly affected by temporal variation in current velocity.

¹Present address: Department of Biology, University of Windsor, Windsor, Ontario. N9B 3P4.

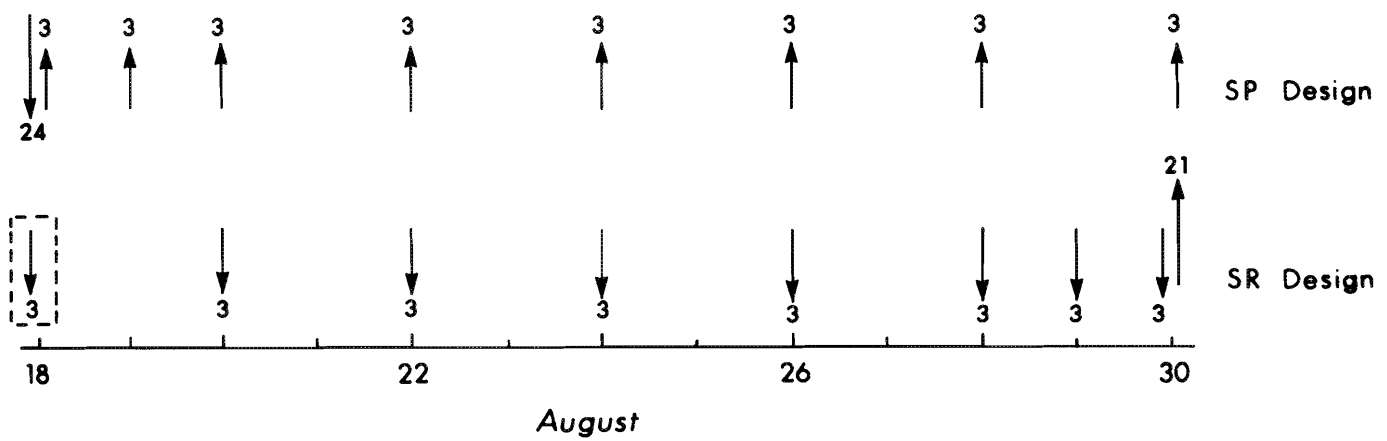


FIG. 1. Schematic outline of August sampling schedule indicating times of placement (downward pointing arrows) and removal (upward pointing arrows). Numerals indicate number of trays placed or removed. Enclosed arrow for SR design indicates trays not actually placed, but common to SP design.

Materials and Methods

The study site was a riffle on the Pembina River, central Alberta (55°36'N, 115°00'W). Here, the river is wide (65 m) and shallow (maximum depth 1.2 m), with substrate of smooth limestone cobble embedded in coarse sand. We have provided a detailed description of a similar site 800 m downstream (Ciborowski and Clifford 1983).

Colonization trays (25 × 25 × 10 cm) were made of 1.27-cm mesh galvanized wire screening filled by shovel with streamside substrate, a naturally occurring mixture of sand, gravel, cobbles, and detrital material. Experiments were conducted in May and August 1980. May trials were to last 30 d. On 14 May, 30 trays were placed in a 5 × 6 grid, each 1 m from any other. The area beneath each tray was thoroughly disturbed by kicking, and removing all large cobbles prior to placement. Depth and mean current velocity (v) (Ott C-1 current meter at 0.6 × depth) above each tray were monitored. Five 0.1-m² Hess samples (Waters and Knapp 1961) were taken to estimate benthic density (B). Three randomly chosen trays were removed after 2 min and after 1, 2, 4, 6, 8, and 12 d. Flooding, which began on the 11th d, prevented further sampling and subsequently resulted in loss of all remaining trays.

Because preliminary data from May indicated very rapid colonization (densities of abundant taxa had stabilized after 2 d), August experiments were conducted over only 12 d. On 18 August 1980, 24 trays were placed at the same site, and 3 were harvested after 2 min. Benthic density in undisturbed areas was estimated from three Hess samples collected 1 and 11 d after initial placement. Groups of three trays were removed on each of days 1, 2, 4, 6, 8, and 10. Except on day 1, they were filled with new substrate and returned to their original locations. Other groups of three trays were set in place on days 11 and 12. All trays were removed on day 12. This procedure provided both SP and SR data series over the 12-d interval. Each consisted of three replicates of samples that had been in place 0, 1, 2, 4, 6, 8, 10, or 12 d (Fig. 1). The 12-d samples were common to both SP and SR data sets. One sample on each of days 8 and 10 of the SR series was partially lost during removal and was not considered in subsequent analyses.

Trays were recovered by sliding a three-sided aluminum box beneath them from upstream. A downstream dip net caught animals dislodged during harvesting. Each sample was trans-

ferred into enamelled pans at streamside. Stones were hand-rubbed to remove adhering material and discarded. The sample was then repeatedly flooded with river water, which, together with organic material, was poured through a 0.210-mm mesh net. Remaining inorganic material was carefully examined for stone-cased organisms before being discarded. Retained material was preserved in Kahles' fluid.

In the laboratory, samples were elutriated to remove any remaining inorganic material. Each sample was sieved into fine (FPOM; <1.00 mm) and coarse (CPOM; ≥1.00 mm) fractions. All animals were sorted beneath a dissecting microscope. The two fractions were then air-dried at room temperature and weighed to the nearest 0.01 g.

Data Analysis

To evaluate the similarity in taxonomic composition between colonization trays and Hess samples, we compared the 10 most abundant taxa collected by each method using Spearman's rank correlation coefficient. Rankings of abundance from colonization trays were estimated from total numbers collected on the 8th (last sampled pre-flood) and 12th d of May and August trials, respectively. These were compared with totals from the 5 May and 6 August Hess samples, respectively. Taxa considered accounted for between 83 and 97% of all individuals collected on the relevant sample dates.

Numbers of animals colonizing trays in August were compared by two-way analysis of variance (ANOVA, Dixon 1981). The two factors tested were time (days 1–10) and design (SP vs. SR). All data were transformed ($\ln(Y + 1)$) to equalize variances among groups. Ten taxa (see Table 1) were abundant enough to be analyzed by this method.

Sheldon (1977) suggested two empirical curves to which colonization data may be fitted: a power curve and an asymptotic ("equilibrium model") curve. We used the asymptotic model because the resulting regression parameters have biological relevance. We used least-squares nonlinear regression analysis (Dixon 1981) to describe colonization of individual taxa according to the formula

$$(1) \quad N_t = N_\infty(1 - e^{-m_e t})$$

where t = days of colonization, N_t = number of animals in colonization trays after t days, and N_∞ and m_e are regression

coefficients; N_{∞} is an estimate of the number of animals to be expected in trays after infinite time, whereas m_e represents turnover, i.e. the proportion of animals that leave a tray each day. This model requires the assumption that N_{∞} and m_e are constant through time.

The influence of current velocity, depth, discharge, FPOM, and CPOM on numbers of individuals colonizing trays independently of time was examined using multiple linear regression. The dependent variable was the residual number of animals of a given taxon in each tray after nonlinear regression against time.

Results

Because the May trial was conducted during a period of declining discharge, current velocity initially decreased over the trays (Fig. 2). Flooding began on the 11th d and subsequently washed away all remaining trays. Water levels rose during August trials, exposing trays to substantially greater current velocities and water depths at the end than at the beginning of the experiment.

There was no pronounced systematic change in detritus concentration in colonization trays during the experiments, although some material accumulated during the first 2 d of SP trials (Fig. 3). Amount of FPOM in trays generally paralleled that in Hess samples. However, CPOM (decomposing twigs and leaves) was more abundant in trays than in undisturbed riverbed substrates.

Trays were rapidly colonized by most taxa collected in Hess samples. Between four and seven taxa were present in colonization trays at the time of placement (day 0, Fig. 4), but in most cases these were represented by only one or two individuals. Numbers of taxa in trays exceeded those in Hess samples after only 1 d. This difference persisted throughout the sampling periods and was evident for both designs.

Although Chironomidae dominated both Hess samples and colonization trays in all study trials, there was no significant association between order of abundance of taxa in trays and Hess samples ($n = 14$, $r_s = 0.16$, $p > 0.05$ in May; $n = 13$, $r_s = 0.33$, $p > 0.05$ in August). Thus, although Hess and tray samplers collected a similar variety of animals, their representation of abundant species differed markedly.

All but two of the taxa analyzed (*Isogenoides elongatus* (Hagen) and *Simulium tuberosum* Lundström) showed significant changes in number with respect to time ($p < 0.05$ by ANOVA). Because both *I. elongatus* and *S. tuberosum* were virtually absent from day 0 trays, we infer that saturation by these animals was achieved within 1 d. Significant differences due to design type were obtained for four taxa (*Baetis tricaudatus* Dodds, *Heptagenia elegantula* (Eaton), *I. elongatus*, *Alloperla* spp.). In all cases, greater numbers colonized during SR than during SP trials. Significant interaction effects were observed for *B. tricaudatus*, *Alloperla*, *S. tuberosum*, and Chironomidae. We interpret this also to be a function of differing colonization patterns among the two design treatments. In all, only 4 of the 10 taxa analyzed showed no design or interaction effect (*Ephemera inermis* Eaton, *Rhithrogena hageni* Eaton, *Isoperla* spp., Hydropsychidae).

Colonization Patterns and Rates

Colonization by all abundant taxa was rapid. Densities of animals in trays after only 1 d approximated or exceeded those estimated from Hess samples. Colonization appeared to be more

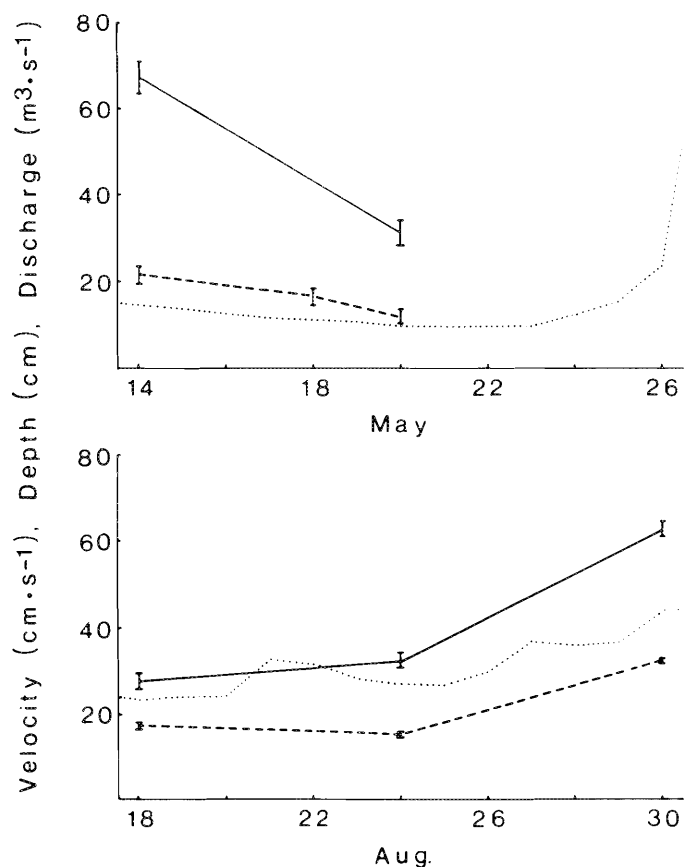


FIG. 2. Mean (± 1 SE) current velocity (—) and depth (---) above colonization trays, and daily river discharge (···).

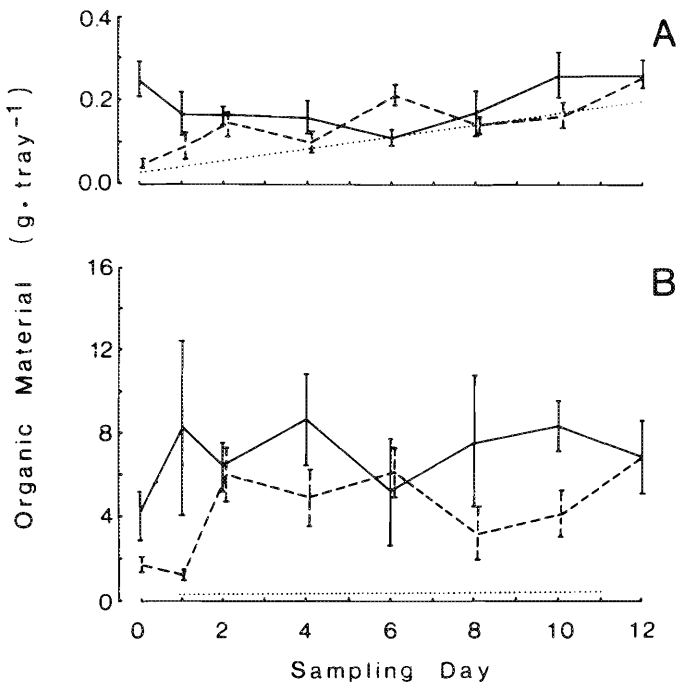


FIG. 3. Mean (± 1 SE) amount of (A) FPOM and (B) CPOM in August colonization trays and Hess samples. —, SR design; ---, SP design; ···, Hess samples.

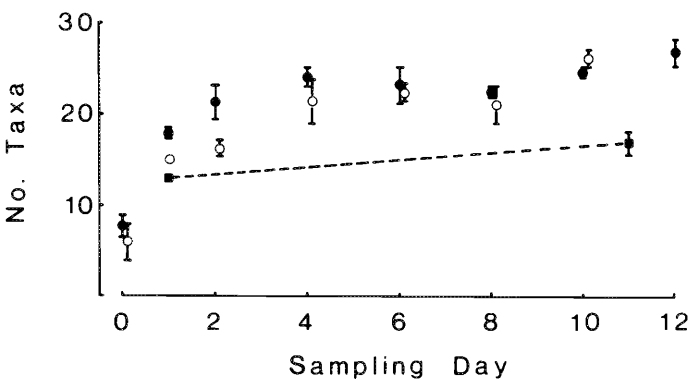


FIG. 4. Mean (± 1 SE) number of taxa collected in August colonization trays (●, SR design; ○, SP design) and Hess samples (■).

rapid in May than in August; although, because life history stages differed, direct comparison is not strictly valid.

The equilibrium model described colonization patterns well in many cases, especially August SR and May trials. However, Hydropsychidae (Fig. 5A) and mayflies collected according to the SP design (Fig. 5B) tended to accumulate in a linear fashion with respect to time. Large stoneflies (*Claassenia sabulosa* (Banks), *I. elongatus* (Hagen), *Pteronarcys dorsata* (Say)) (Fig. 6) appeared in trays so rapidly that numbers did not vary over the course of sampling. *Baetis tricaudatus* (May), Hydropsychidae (May), and *Simulium* (Fig. 7) were unique in reaching maximum abundance within 1–4 d and then declining in numbers.

Regression estimates of m_e (emigration) ranged from zero for taxa whose colonization was a linear function of time to over 0.65 for mayflies that predominate in drift in the Pembina River (*R. hageni*, *E. inermis* in May; Table 1). Inadmissible emigration estimates ($m_e > 1.0$) occurred for taxa whose abundances peaked and subsequently declined. Estimates for SP observations were equal to or smaller than SR observations for all taxa analyzed except Chironomidae.

None of the other variables examined (velocity, depth, discharge, CPOM, FPOM) significantly reduced residual variation among samples for any of the taxa examined ($p > 0.05$). Evidently, any significant variability attributable to these factors was systematic and related to temporal rather than to spatial variation.

Modification of the Equilibrium Model

The SR sample schedule most frequently produced curves corresponding in shape to the equilibrium model, possibly because this design more closely met the model assumptions of constant numbers immigrating (K) and constant likelihood of emigration (m_e). However, because both K and m_e are largely determined by animals' drift tendencies (Townsend and Hildrew 1976; Williams and Hynes 1976) and drift is often strongly dependent on prevailing current velocity, which varied markedly during the trials, one should not expect these factors to be constant.

To estimate the sensitivity of perceived colonization pattern to temporal variation in current velocity, we modified the model to express its components in terms of drift as related to current velocity.

Sheldon's (1977) equilibrium model postulates that change in numbers in a colonization tray over time (dN/dt) reflects the

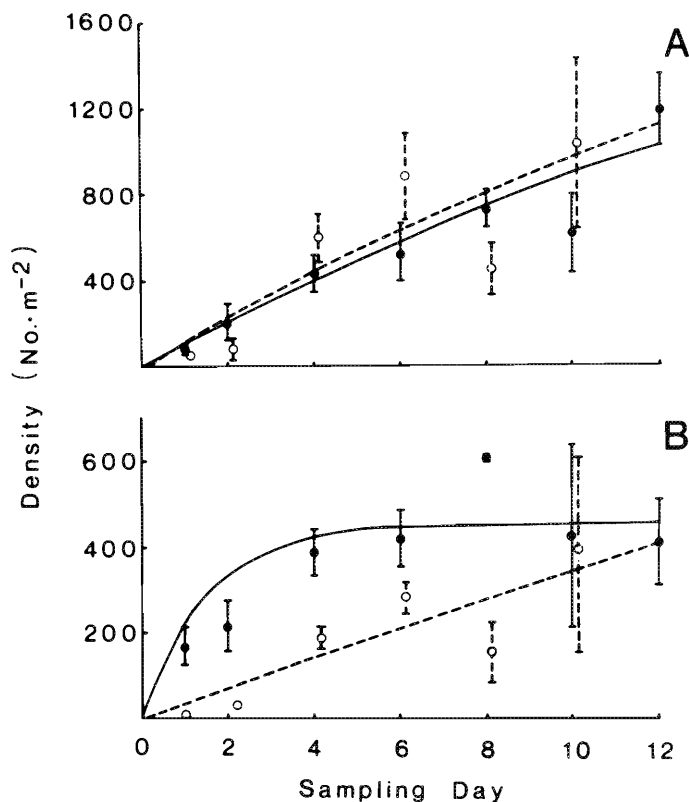


FIG. 5. Colonization of trays by (A) Hydropsychidae in August (B) *B. tricaudatus* in August. Lines are regression estimates; points and intervals are means (± 1 SE). —, SR design; ---, SP design.

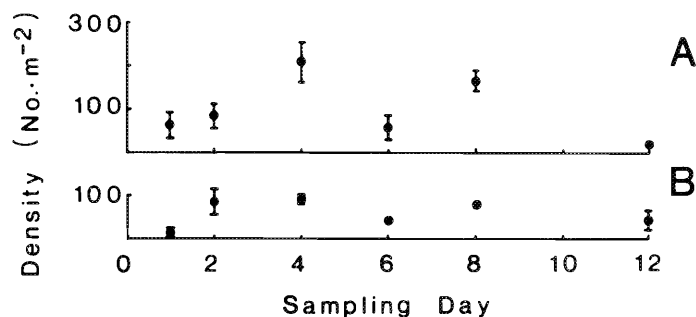


FIG. 6. Mean (± 1 SE) density of (A) *C. sabulosa* and (B) *P. dorsata* collected in trays during May.

difference between number of animals immigrating per day (K) and the proportion of animals in the tray that emigrate (m_e):

$$(2) \quad dN/dt = K - m_e N.$$

(In the integrated form of the equation, $N_\infty = K/m_e$.) We will designate m_i and m_e as the daily proportion of animals that enter the drift in the river itself and from colonization trays, respectively.

The magnitude of K will depend on both the number of animals carried over a colonization tray and on individuals' ability to land successfully. We assume that the riverbed is uniform upstream of the trays and that the daily proportion of animals departing from the substrate (m_i) is homogeneous. The number of animals departing from each upstream region is thus $B \cdot m_i$ (upstream benthic density \times proportion departing). Drifting animals settle randomly as they are carried downstream, with a species-specific settling rate (r). The equilibrial

TABLE 1. Regression coefficients and coefficients of determination relating number of individual macroinvertebrates per tray to time.

Taxon	Date	SP			SR		
		<i>N</i>	<i>m_e</i>	<i>R</i> ²	<i>N</i>	<i>m_e</i>	<i>R</i> ²
<i>Baetis tricaudatus</i>	May	12.0	1.936	0.02	—	—	—
	Aug.	248.8	0.009	0.46	28.6	0.683	0.28
<i>Ephemera inermis</i>	May	70.1	0.673	0.35	—	—	—
	Aug.	500.0 ^a	0.003	0.59	500.0 ^a	0.003	0.54
<i>Heptagenia elegantula</i>	Aug.	133.0	0.006	0.48	10.6	0.187	0.36
<i>Rhithrogena hageni</i>	May	28.2	0.537	0.48	—	—	—
	Aug.	86.2	0.029	0.49	38.1	0.113	0.70
<i>Claassenia sabulosa</i>	May	8.8	0.679	0.22	—	—	—
<i>Isogenoides elongatus</i>	Aug.	4.5	0.229	0.09	5.1	0.666	0.21
<i>Isoperla</i> spp.	Aug.	31.4	0.260	0.39	28.1	0.375	0.42
<i>Alloperla</i> spp.	May	128.8	0.258	0.66	—	—	—
	Aug.	218.3	0.031	0.85	91.4	0.116	0.81
Hydropsychidae	May	22.3	1.176	0.13	—	—	—
	Aug.	183.4	0.041	0.55	172.1	0.040	0.75
Chironomidae	May	670.2	0.178	0.72	—	—	—
	Aug.	136.5	0.153	0.55	129.4	0.083	0.46
<i>Simulium</i> spp.	Aug.	23.6	0.906	0.03	24.1	2.562	0.01

^aValue undefined; regression fitted to limit value of 500.

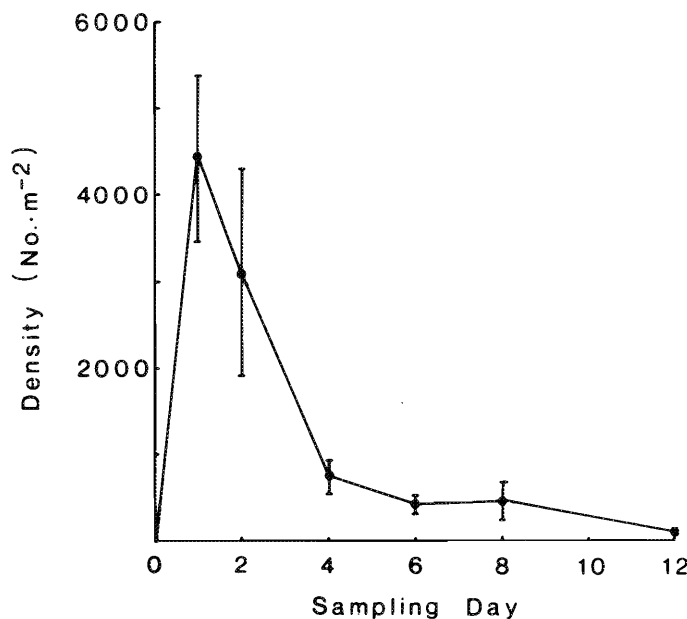


FIG. 7. Mean (± 1 SE) density of *S. tuberosum* collected in trays during May. Lines were fitted by eye through means.

number of animals (Y_{\max}) that will travel past a line across the river is (McLay 1970; Elliott 1971)

$$(3) Y_{\max} = B \cdot m_i \cdot r^{-1}.$$

Furthermore, the number of suspended animals that will settle per unit distance downstream is $Y_{\max} \cdot (1 - e^{-r})$ (Elliott 1971). Hence,

$$(4) K = Y_{\max} \cdot (1 - e^{-r}) \\ = B \cdot m_i \cdot r^{-1} \cdot (1 - e^{-r}) \\ = B \cdot m_i \cdot \frac{(1 - e^{-r})}{r}.$$

Substituting in equation (2),

$$(5) dN/dt = B \cdot m_i \cdot \frac{(1 - e^{-r})}{r} - m_e \cdot N.$$

Integration produces

$$(6) N_t = B \cdot \frac{m_i}{m_e} \cdot \frac{(1 - e^{-r})}{r} \cdot (1 - e^{-m_e t}).$$

Current velocity can affect both r and m_e and hence N_t , as shown in the second and third groups of terms in equation (6). The relation between r and current velocity (v) is species specific but generally hyperbolic (Elliott 1971; Ciborowski and Corkum 1980; Ciborowski 1983a). Consequently, at low current velocities, r is relatively large and $(1 - e^{-r})/r$ is small. As current velocity increases, r rapidly decreases to an asymptote and $(1 - e^{-r})/r$ approaches 1. Thus, this term only becomes an important consideration at relatively low velocities ($< 15 \text{ cm} \cdot \text{s}^{-1}$; J. J. H. Ciborowski, unpubl. data).

The relationship between v and immigration and emigration likelihoods is more complicated because drift probability can be either a positive or a negative function of current velocity, depending on the species and developmental stage examined. Many taxa are more prone to depart from the substrate at high current velocities than at low (Elliott 1967; Waters 1972); however, the reverse is often true for rheophilic organisms such as *Baetis* mayflies (Corkum et al. 1977; Ciborowski 1983b). If immigration and emigration are equal, the magnitudes of m_e and m_i will not affect the ultimate size of N after long periods, but they will affect the rate at which N approaches its maximum.

The formulation of equation (6) stipulates that N_t can never exceed B when $m_e = m_i$. In fact, the number of organisms in newly placed trays frequently exceeds benthic density in adjacent undisturbed regions (Rosenberg and Resh 1982; this study). Consequently, organisms must be, at least initially, less prone to depart from colonization trays than they are from other upstream undisturbed substrates (i.e. $m_e < m_i$). As colonization substrates become qualitatively more similar to undisturbed regions, m_e will become more similar to m_i . The rate of approach to equality will depend on the sensitivity of individual

TABLE 2. Equations relating daily proportion of *B. tricaudatus* individuals departing from substrate (m_i), instantaneous settling rate (r), and upstream benthic density (B) to mean current velocity (v).

Condition	Departure	Settling	Benthic density
Living	$m_i = 0.94 - 0.0087v$	$r = 8.02v^{-1.066}$	$B = -18.8 + 3.105v$
Dead	$m_i = -0.05 + 0.0063v$	$r = 3.43v^{-1.129}$	$B = -18.8 + 3.105v$

TABLE 3. Regression coefficients and coefficients of determination relating hypothetical numbers of living and dead animals colonizing trays to time under various current velocity regimes, and actual emigration rates (m_e), immigration rates (m_i), and upstream benthic density (B) on last day of sampling.

Condition	Benthic density	Velocity regime	Regression								
			SP			SR			Actual		
			N_∞	m_e	R^2	N_∞	m_e	R^2	m_e	m_i	B
Living	Constant	Constant	267	0.314	0.95	267	0.314	0.95	0.285	0.597	100
	Constant	Increasing	274	0.348	0.95	293	0.224	0.95	0.189	0.394	100
	Constant	Decreasing	266	0.230	0.94	258	0.387	0.91	0.333	0.697	100
	Increasing	Increasing	319	0.151	1.00	307	0.329	0.95	0.189	0.394	175
	Decreasing	Decreasing	242	0.516	0.71	210	0.312	0.95	0.333	0.697	68
Dead	Constant	Constant	253	0.141	0.99	253	0.141	0.99	0.141	0.296	100
	Constant	Increasing	324	0.076	1.00	205	0.247	1.00	0.211	0.442	100
	Constant	Decreasing	226	0.241	1.00	448	0.053	1.00	0.107	0.224	100
	Increasing	Increasing	600 ^a	0.003	0.95	223	0.358	0.99	0.211	0.442	175
	Decreasing	Decreasing	238	0.459	0.95	600 ^a	0.003	0.97	0.107	0.224	68

^aValue undefined; regression fitted to limit value of 600.

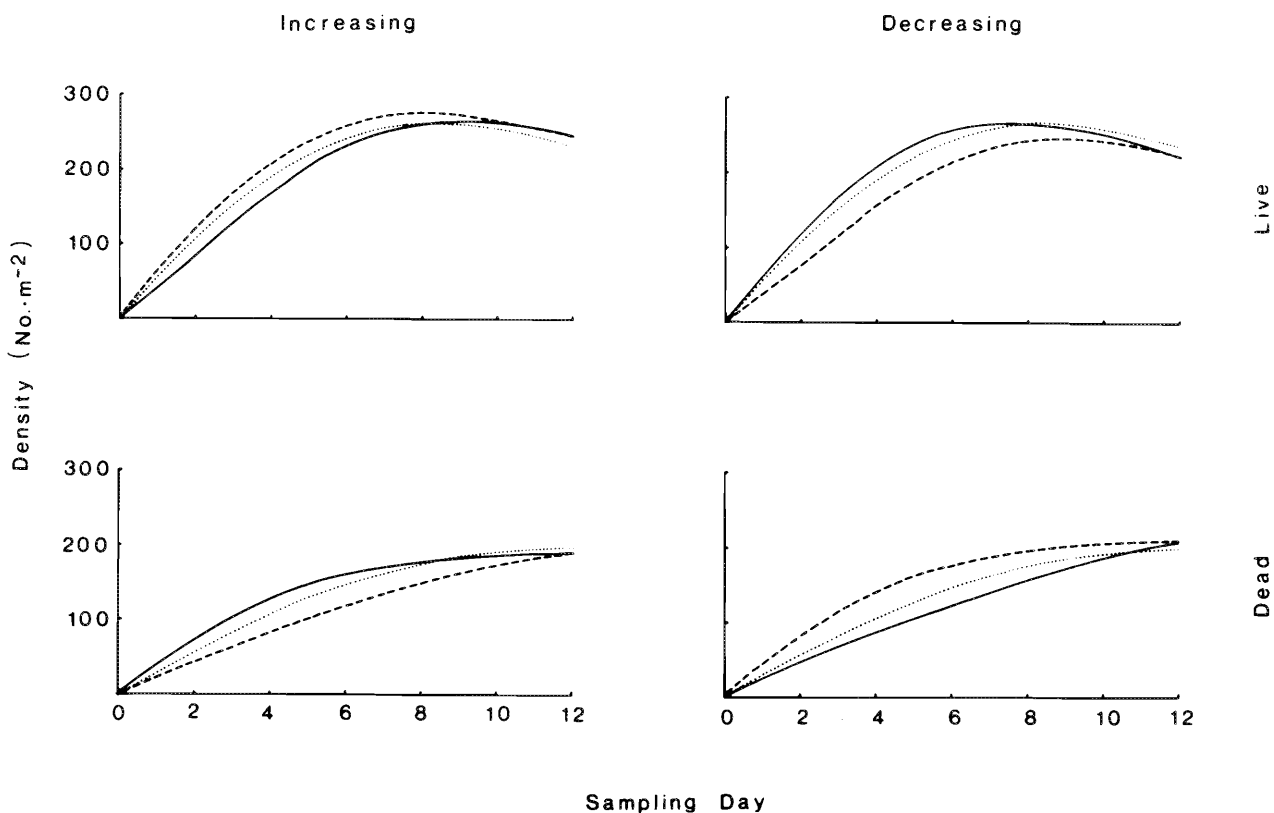


FIG. 8. Hypothetical colonization curves for living (upper) and dead (lower) *B. tricaudatus* larvae under increasing (left) and decreasing (right) current velocity regimes; benthic density (B) held constant. —, SR design; ---, SP design; ···, current velocity constant. Lines were fitted by eye through points.

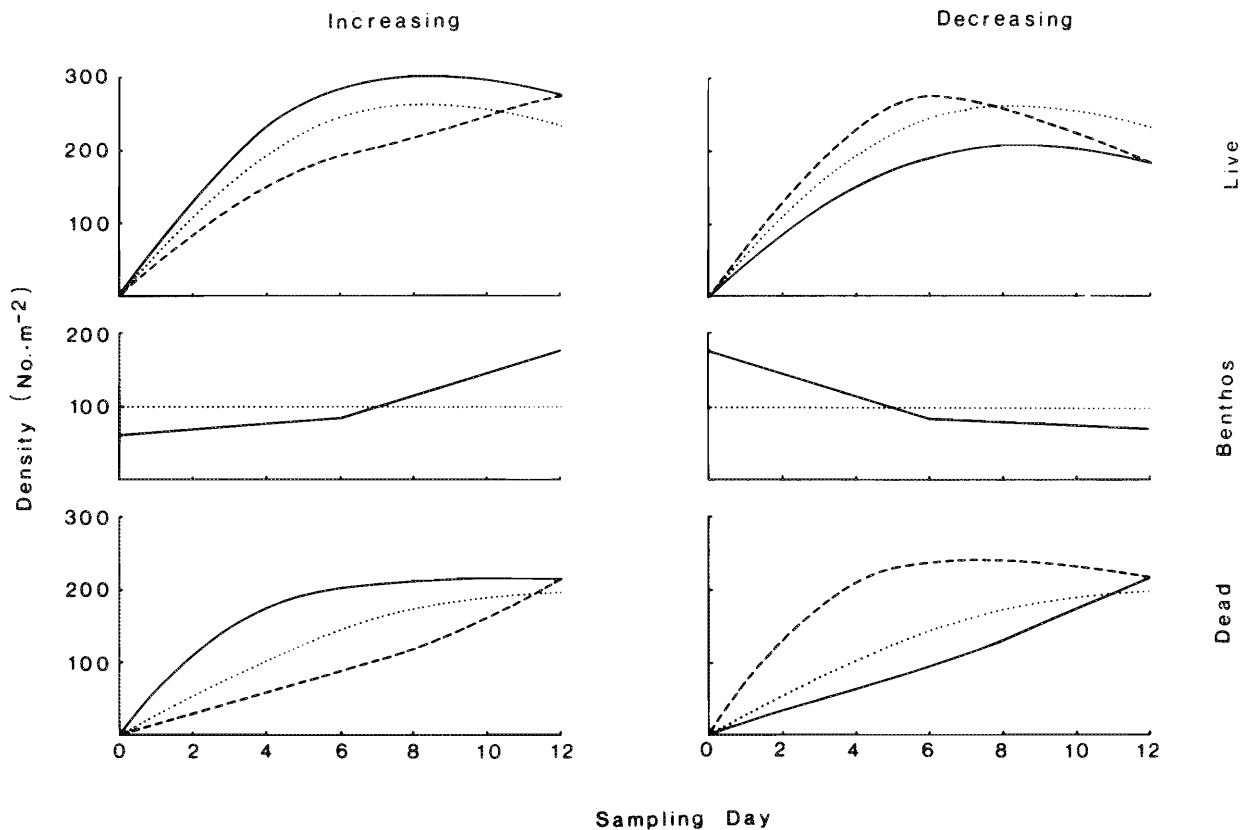


FIG. 9. Hypothetical colonization curves for living (upper) and dead (lower) *B. tricaudatus* larvae under increasing (left) and decreasing (right) current velocity regimes, with benthic density (B) varying as shown in centre panels. —, SR design; ---, SP design; ···, current velocity constant. Lines were fitted by eye through points.

taxa to environmental parameters and on potential inter- and intra-specific interactions. For example, *S. tuberosum* larvae predominate on clean rock surfaces in the Pembina River. Such surfaces rapidly accumulate silt, periphyton, and FPOM in spring, and this is presumably reflected in a rapid decline in the $m_i:m_e$ ratio (Fig. 7). The pattern of decline of animals in this instance suggests an exponential relationship such that m_e might be expressed as

$$(7) \quad m_e = m_i \cdot (1 - e^{-ct})$$

where c is the instantaneous rate of change of tray suitability. In this case, equation (5) could be reformulated as

$$(8) \quad dN/dt = B \cdot m_i \cdot \frac{(1 - e^{-r})}{r} - m_i \cdot (1 - e^{-ct}) \cdot N.$$

To evaluate equation (8) under various flow conditions, we used laboratory and field data pertaining to the drift and settling ability of living and dead *B. tricaudatus* larvae from the Pembina River (Ciborowski 1983a, 1983b). Departure of live animals of this species from the substrate is a negative linear function of current velocity, and individuals can settle rapidly, whereas dead animals are carried off as a positive function of current and settle slowly, in a manner analogous to that of taxa with little mobility, such as Chironomidae. Benthic density (B) also varies with current velocity, a result of larvae moving laterally in the river as water levels rise and fall (Ciborowski and Clifford 1983). We used equations relating daily departure likelihoods (m_i), instantaneous settling rates (r), and benthic density (B) of these animals to current velocity (Table 2) to predict hypothetical colonizing patterns during periods of

increasing, decreasing, and constant mean current velocity by both SP and SR procedures. Equation (8) was used to estimate expected colonization at 1-d intervals for 12 d, given the current velocity regime recorded during August trials (increasing flow). To determine the influence of decreasing velocity, the order of August readings was reversed. We also evaluated expected colonization pattern with current velocity constant, set at the overall mean value observed during August trials ($38.25 \text{ cm} \cdot \text{s}^{-1}$). Benthic density (B) was $100 \text{ individuals} \cdot \text{m}^{-2}$ when held constant, or averaged $100 \text{ individuals} \cdot \text{m}^{-2}$ when allowed to vary. A substrate conditioning factor (c) of 0.05 was arbitrarily chosen. At this conditioning rate, m_e would be 90% of m_i within 46 d. The resulting colonization patterns were analyzed by nonlinear regression as described for field trials.

When current velocity was held constant, SR and SP designs provided identical results, and regression estimates of m_e were similar to actual values at the end of the experiments (Table 3). However, when velocity fluctuated, whether or not benthic density was permitted to vary, the shape of colonization curves changed appreciably. If benthic density was held constant, approximately linear increases in numbers were observed for dead animals analyzed by SP methods when current increased and by the SR method when velocity decreased (Fig. 8). Any change in current velocity produced regression estimates of m_e and N_∞ that were markedly different from values determined from constant velocity trials, even though all regressions accounted for a large amount of total variation (Table 3).

Permitting B to vary with current velocity magnified the differences between SP and SR designs (Fig. 9). In these cases, the state of animals (alive or dead) was of less consequence than the direction of change in current velocity. The SR design

produced large overestimates of m_e when velocity increased and underestimates when velocity decreased. The patterns generated for live animals under increasing current velocity conditions were consistent with those for *B. tricaudatus* larvae in August (Fig. 5B). Furthermore, the curve for live animals generated from the SP design during decreasing flow corresponded in shape to colonization patterns of most taxa during the May (SP) field trial.

Discussion

On a density per unit area basis, colonization traps were several times more effective in collecting aquatic invertebrates than Hess samples. This has been frequently reported (see Rosenberg and Resh 1982) and may partly reflect the greater amount of usable area available within the uncompacted substrate of the trays (Rabeni and Minshall 1977; Shaw and Minshall 1980). However, the taxonomic composition of the trays corresponded poorly with the local benthic community indicated by Hess samples. Colonization trays generally contained a wider variety of animals and substantially different proportions of individuals of common taxa. This probably represents the large contribution made by drifting animals from outside the immediate sampling area; these typically immigrate in proportions other than those represented by benthic samples (Waters 1972).

Simultaneous placement and simultaneous removal designs gave significantly different results for 6 of the 10 taxa analyzed in August. We anticipated that the problems of temporally varying physical conditions and changing community composition would be minimized by use of the SR design because all trays would have been exposed to the same current velocity regime and populations. The SR design did produce results more consistent with the equilibrium model (fewer turnover estimates were inadmissible). However, results of our hypothetical data manipulations suggest that this outcome was fortuitous. We postulate that the potential influence of daily variation in current velocity on both emigration likelihood and benthic density is so great that neither the SP nor the SR design alone can provide reliable measures of colonization patterns. Note, however, that the regression estimates of colonization variables for the two designs consistently enclosed the constant velocity values. Thus, concurrent use of the two sampling schedules should indicate conservative upper and lower limits of daily turnover. Furthermore, the magnitude of difference between the estimates of m_e should be a measure of the sensitivity of taxa to the variation in conditions during the study.

Our results lead us to question the validity of colonization samplers as tools to monitor lotic communities. Although trays collect many taxa, the individuals encountered include the fauna of habitats other than that in the immediate area. Furthermore, most taxa are overrepresented in trays and relative abundance corresponds poorly with densities in natural substrate. Although our trials were restricted to 12 d, there is little evidence that exposure of trays for longer periods improves the correspondence (Meier et al. 1979; Shaw and Minshall 1980; Rosenberg and Resh 1982). Because frequent sampling trips are expensive and there is an inherent danger of losing trays to floods or vandals, we question the utility of colonization sampling relative to standard quantitative (Hess) or even qualitative (kick net) sampling techniques. We concur with Rosenberg and Resh (1982) that colonization samplers are a necessary alternative when sampling habitats inaccessible by usual benthic collecting

methods, but caution that precision of colonization sample estimates (variation among samples) should not be taken as indicative of accuracy (representativeness).

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