

Temporal patterns in recolonization of stream benthos

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With 11 figures in the text

Abstract

Recolonization patterns of stream benthos were studied over one year using implanted substrates. Relatively low numbers of individuals and species colonized in the winter months (December—March) compared with the summer months (June—September). This was most likely the result of water temperature. There was a negative correlation between numbers of animals colonizing each month and water depth, but no correlation with amounts of either FPOM or CPOM settling in the substrates. Annual recolonization curves for individual species revealed several different patterns. Discontinuities in the curves of some species suggested variation in seasonal mobility, probably associated with a specific stage in the life cycle. Mass movements were particularly evident in first instar larvae of many insect species and this supports the theory of "distributional drift". Many of the colonizing species showed clumped distributions which may have resulted from a superabundance of detrital food in the stream. Variations in the settling of inorganic materials on the substrates were also evident over the year. The relevance of the findings of this study to interpretation of data collected by artificial substrate techniques is discussed.

Introduction

Certain age or size classes of benthic invertebrate species take part in population movements out of proportion to their density in the benthos (ULFSTRAND et al., 1974). Their presence in surface drift, rather than just above the substrate, suggests an active determination to move (LARIMORE, 1972). Taxa that exhibit strong diel drift patterns, e.g. *Gammarus* and *Baëtis*, are readily able to return to the substrate (CIBOROWSKI & CORKUM, 1980). These and many other studies point to a behavioural component of movement of animals within streams (see WATERS, 1972 and MÜLLER, 1974). This component may differ in its intensity between species and may be superimposed, on occasion, by abiotic factors, such as flow, light and temperature; the latter two affecting the animals' physiology. By studying recolonization by a natural stream community over a year, it should be possible to detect patterns of movement, resulting from interactions of both biotic and abiotic influences, that will provide useful information on the temporal nature of benthic communities.

Study Area

The study area is a 15 m long riffle on the upper, east branch of Duffin Creek, Durham County, Ontario (43° 58' N; 79° 05' W). Depth on the riffle varied between 20 cm in midsummer and 60 cm during the spring runoff, while waterflow over the year ranged from 25 cm/s to 110 cm/s. The substrate consists of mixed gravels with some sand and clay patches underlain by clay at a depth of approximately 20 cm. Flat cobbles, up to 20 cm in diameter, are commonly embedded near the surface. Further description of this stream is given by WILLIAMS (1980).

Materials and methods

Baskets, measuring 30 × 30 × 15 cm deep, and made of 1 cm² wire mesh, were lined with 0.023 cm² mesh plastic mosquito screening. To each was added approximately 20.5 kg of sterilized gravel substrate of uniform particle size (3.2 cm diameter; heterogeneity = 1.0 = grain size 60 %/gs 10 %, see method of SCHWOERBEL, 1961). A low heterogeneity substrate was chosen to minimize any variation between the replicates which might have arisen due to unequal mixing of a range of gravel sizes in each basket. It is probable that the uniformity of this substrate discouraged colonization by certain species (see WILLIAMS & MUNDIE, 1978 and WILLIAMS, 1980) but it was felt that most of the common taxa would be represented.

At the beginning of each month, for one year (November 1977—October 1978) three baskets were nestled into the substrate across the middle of the riffle and left to colonize. Sufficient distance was allowed between them to prevent interference. At the end of each month they were lifted, whilst holding a 53 μm mesh nitex net underneath to prevent loss of contents, and replaced with three new baskets. Organic and inorganic contents of the baskets were removed by repeated washing with water and preserved in 5 % formalin. Current, incident radiation, depth and maximum and minimum water and air temperatures were measured throughout the year.

In the laboratory, the contents of each basket were subsampled by the method of MUNDIE (1971), and the animals and coarse particulate organic matter-CPOM (particles > 1 mm) were picked from the residue (fine particulate organic matter-FPOM, particles < 1 mm; and inorganic particles). A subsample of at least 500 animals was counted and identified from each basket. Estimates of the composition of inorganic and organic particles that had collected in the substrates over each colonization period were made by the procedure described in WILLIAMS (1980).

In analysis of the data, this study assumes that the substrates retrieved from the riffle each month contained numbers and varieties of animals that reflected the mobility of the riffle community during the previous four weeks. Only in the case of species with very fast, multivoltine life cycles might this assumption be wrong. However, even for these, construction of life cycle histograms, such as for *Dolophilodes distinctus* (WILLIAMS & WILLIAMS, in prep.), showed that very few stages had not been collected in the substrates. Plotting the monthly values consecutively should result in a legitimate pattern of recolonization over the year. No estimate of distance travelled before reaching the baskets has been attempted.

Results

Physical parameters for east Duffin Creek are given in Fig. 1. Current varied from about 25 cm/s under ice in January to a maximum near 100 cm/s in March, April and October. There was a gradual increase in current from late spring to late summer. Maximum and minimum water temperatures followed the same pattern as air temperature, although with a reduced amplitude. Ranges were least during the winter months and greatest during the spring, summer and fall. The annual range was from -2.0°C to 24.4°C .

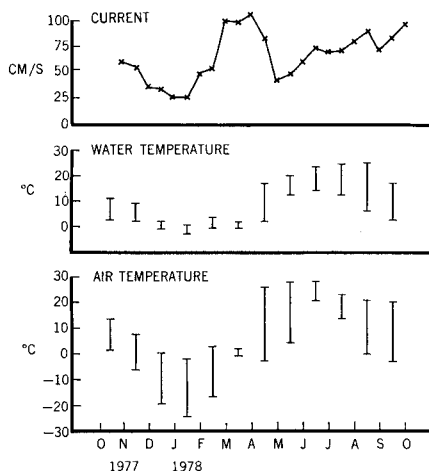
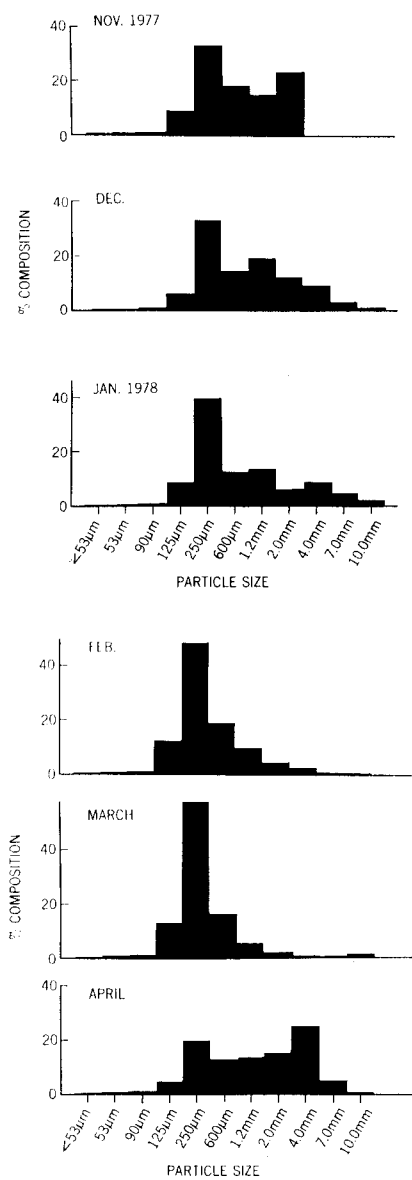


Fig. 1. Physical parameters for Duffin Creek (1977—1978).

Fig. 2 A-L gives the size composition of the inorganic sediment collected in the colonization baskets at the end of each month. In general, the total weight of sediment did not correlate with the bimonthly current readings, although peak values coincided during the April runoff period. However, seasonal patterns in sediment composition are evident. During low flow conditions in winter (December—February) the composition of the sediment remained fairly similar. At the end of March, a slightly greater proportion of particles in the $250\ \mu\text{m}$ size class had been deposited. In April and May, larger proportions of particles of $2.0\ \text{mm}$ or greater were collected, presumably due to the high flow in April and early May. The low to moderate flow conditions of the summer months (June—August) saw the increased deposition of particles less than $125\ \mu\text{m}$. Moderate to high flow in the autumn (September—November) resulted in the collection of particles predominantly greater than $125\ \mu\text{m}$.

CPOM and FPOM collections over the year are shown in Fig. 3 A and B. Although the variations in amount of materials collected in the three baskets were high for most months, there seemed to be a trend for both to accumulate in large quantities during the spring runoff. Both declined in abundance during midsummer and increased in the autumn. The large accumulation of CPOM in October was due to newly fallen riparian leaves,



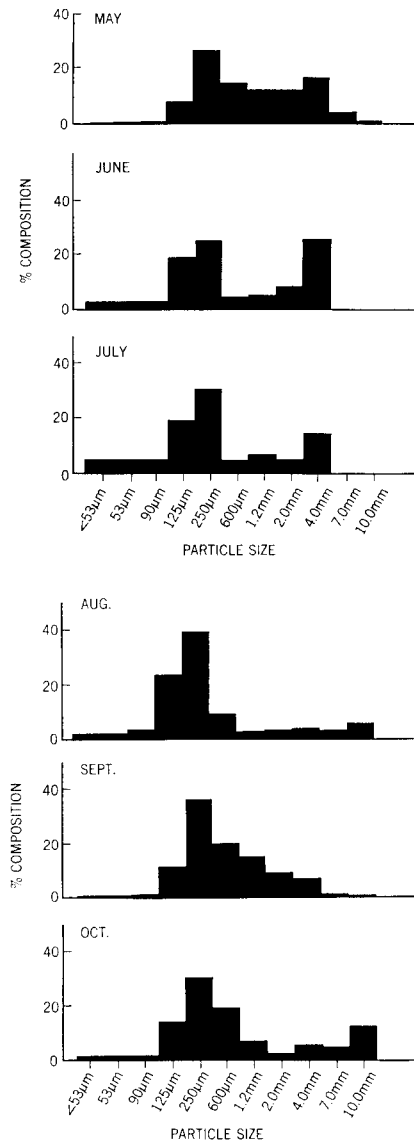


Fig. 2. Percentage composition of inorganic sediment collected by artificial substrates each month.

but even so the accumulation in the baskets was quite patchy. Its composition changed throughout the year (Fig. 3 A). The high values of FPOM in August may have been due to release of particles broken down from CPOM on the streambed during the warm water period and/or sloughing off of periphyton.

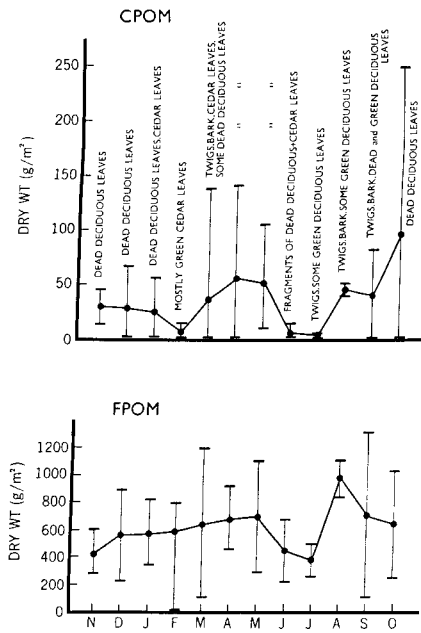


Fig. 3. Amounts of CPOM and FPOM collected by artificial substrates each month.

The pattern of colonization of the baskets by the total benthos over the year is shown in Fig. 4 (expressed as numbers/m² on a semi log scale for convenience). Perhaps the two most obvious features of this are: the relatively low numbers of animals moving onto the baskets during the winter months (December—March) compared with the high numbers during the summer (June—September) and the very wide confidence intervals around the mean values. The numbers of animals are roughly divisible into groups where the upper and lower deviations from the mean are at least 62% (range 62—123%) from December to March, or less than 62% (range 21—61%) from April to November — although August is an exception (76%).

The annual pattern of colonization by the total benthos correlates positively with maximum water temperature ($r = 0.899$, $p < 0.001$) and minimum water temperature ($r = 0.857$, $p < 0.001$), and negatively with stream depth ($r = -0.63$, $p < 0.05$). It does not correlate with current or the monthly accumulations of FPOM or CPOM ($r = 0.348$, 0.131 and 0.086 , respectively). Because of the large variance for the mean numbers of animals per basket, statistical analyses were done on transformed data ($\log x$) (ELLIOTT, 1971).

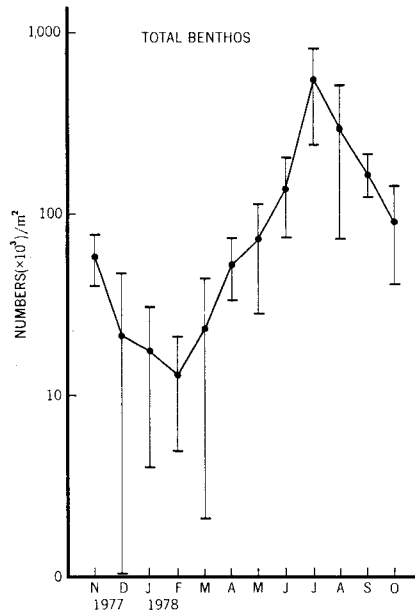


Fig. 4. Annual recolonization curve for total benthos (means of three baskets and 95 % confidence limits are plotted on a semi-log scale).

The numbers of taxa moving onto the baskets are shown in Fig. 5. This curve correlates with both maximum and minimum water temperatures, although more closely with the former ($r = 0.736$, $p < 0.01$; $r = 0.665$, $p < 0.05$, respectively). The curve can be divided into two parts at a point between March and April, when a large temperature change took place. Between November and March, when the maximum water temperature was usually below 5°C , there were generally low numbers of taxa in the baskets, while from April to October, when the minimum water temperature was largely above 5°C , a greater diversity of animals moved onto the baskets.

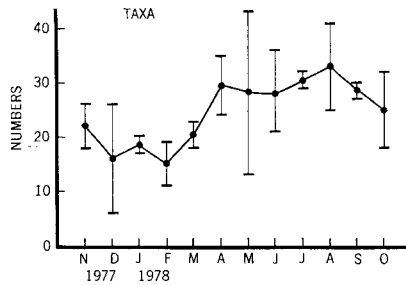


Fig. 5. Variation in number of taxa recolonizing substrates over the year (means of the three baskets and 95 % confidence limits).

The annual recolonization curves for various taxa revealed some interesting patterns. *Nais simplex* PIQUET, *Baëtis* spp. and the chironomids *Rheotanytarsus* spp. and *Corynoneura* spp. have curves that are quite similar to that of the total benthos (Pattern I). The curves for *N. simplex* and *Rheotanytarsus* spp. are shown in Fig. 6 A and B. *N. simplex* showed considerable variation in its density on the baskets throughout the year. If we accept wide confidence limits ($S^2 > \bar{x}$) as an indication of clumped

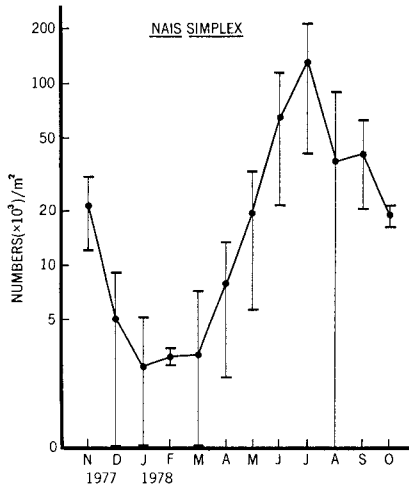


Fig. 6 A. Annual recolonization curve for *Nais simplex* (means of the three baskets and 95 % confidence limits are plotted on a semi-log scale).

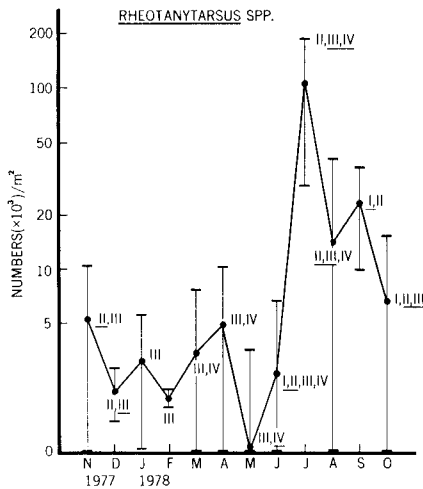


Fig. 6 B. Annual recolonization curve for *Rheotanytarsus* spp. (larval instars are indicated in roman numerals; dominant instars are underlined).

distribution in the baskets, and tight limits ($S^2 < \bar{x}$) to be indicative of homogeneous distribution (ELLIOTT, 1971) then it appears that for most of the year its distribution was clumped, but in February it was more uniform.

The curve for *Rheotanytarsus* undoubtedly represents two species. Throughout the winter and early spring both species grew slowly. Fourth instar larvae were present in reduced numbers on the baskets in May when the species emerged. Predominantly first and second instar larvae of a summer generation of both species colonized the baskets in June but densities were low. By July, however, third and fourth instars were present in large numbers suggesting that these stages were more mobile. A second emergence must have occurred towards the end of July, as by August, small individuals of one species were evident. Early instar larvae of the second species did not appear on the baskets until September. Both species occurred on the baskets at relatively low densities during the winter. One of the interesting features of the colonization by these two species is that they moved onto the baskets throughout the year. Such mobility is perhaps surprising for animals that invest considerable time and energy in building complex, and presumably long-lasting, fixed dwelling tubes and feeding structures.

Ephemerella subvaria McDUNNOUGH, *E. deficiens* MORGAN and the chironomid *Thienemaniella* show a common colonization curve (Pattern II). *E. subvaria* (Fig. 7) as medium to large nymphs, was clumped in its distribution on the baskets during most of the winter. As predominantly large nymphs it was randomly distributed following colonization in March, but

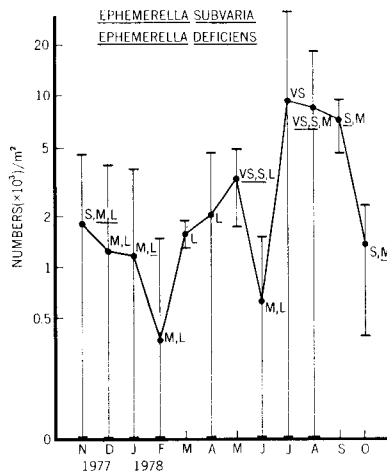


Fig. 7. Annual recolonization curve for *Ephemerella subvaria* and *E. deficiens* (larval size is approximated by the categories — very small, small, medium and large; dominant sizes are underlined).

the same sized nymphs were then clumped in April, after which they emerged. Very small individuals appeared in large numbers, contagiously distributed, in July and reappeared in large numbers while growing in August and September. Recolonization by medium-sized nymphs continued in the fall but at a reduced density. *E. deficiens* did not appear on the baskets until May when early instars colonized in considerable numbers. Medium and large nymphs colonized in June and these must then have emerged as large numbers of very small nymphs appeared in clumps along with *E. subvaria* in July. Many of these nymphs recolonized the baskets in August and September, after which, still in their early instars, they failed to reappear.

Pattern III colonization curve was exhibited by the nematodes and the chironomids *Polypedilum* spp. Colonization by nematodes was generally low over the winter months but increased gradually through the spring to reach a peak during July (when most were very small), August and September. Distributions were clumped over the entire year.

Small numbers of first and second instar *Polypedilum* larvae moved onto the baskets in November, while only second instars did so, at very low densities, all through the winter (Fig. 8). Greater numbers of third instars of species 1 colonized in April and these became common on the baskets, as final instars, by June alongside third instars of species 2. Huge numbers of first instars of a new generation of species 1 colonized in July as did large numbers of final instars of species 2. Both populations were clumped. During August, second instars of species 1 occurred with pre-emergent larvae of species 2. The September substrates contained what must have been first instars of a new generation of species 2 but some second in-

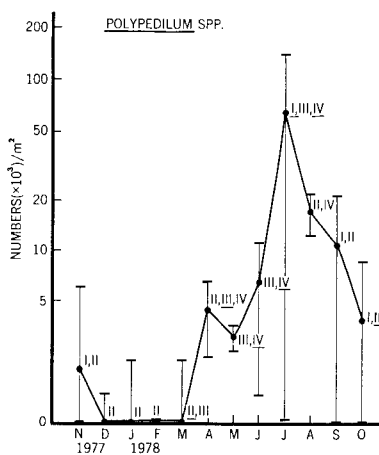


Fig. 8. Annual recolonization curve for *Polypedilum* spp. (larval instars are indicated in roman numerals).

stars of species 1 were also present. By October, the number of colonizers was dropping back to low winter levels.

Remaining species exhibited patterns that were unique. For example, the chironomid *Cricotopus/Orthocladius* sp. (Fig. 9) did not occur on the artificial substrates during November to January, although it clearly must have been in the stream. Predominantly third instar larvae colonized during February to April, there was a drop in the number of third and fourth instars in May, and a large migration onto the baskets in June. No larvae appeared in July or August, but first and second instars colonized in September. If the fall and winter pattern of 1977 was to be repeated, the third and fourth instars found in October would presumably become inactive as winter progressed.

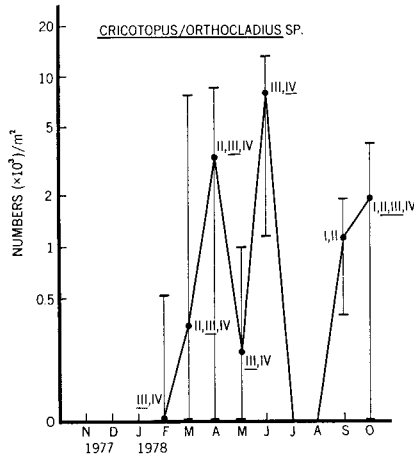


Fig. 9. Annual recolonization curve for *Cricotopus/Orthocladius* sp.

The net-spinning caddisfly *Dolophilodes distinctus* (WALKER) also failed to move onto the baskets during part of the year (Fig. 10). Its numbers were very low until May when first, second and third instars colonized in large numbers. During June, the colonizers were primarily fourth and fifth instars and pupae. A new generation of first and second instars colonized during July and huge numbers of all instars moved onto the substrates in August. Numbers fell rapidly during September and October when the last four instars were common. The few larvae collected during the winter were third and fourth instars. Some winter emergence may have taken place (Ross, 1944). This species is known to feed on FPOM (WALLACE & MALAS, 1976) but its densities on the baskets did not correlate with this parameter. However, the maximum density, in August, coincided with the peak in FPOM.

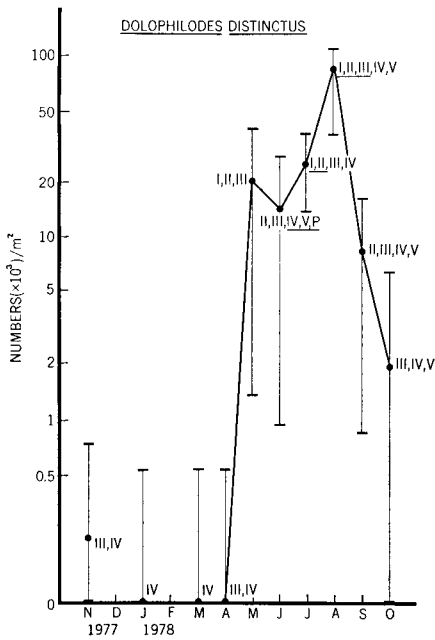


Fig. 10. Annual recolonization curve for *Dolophilodes distinctus* (instars I—V and pupae (P) are indicated).

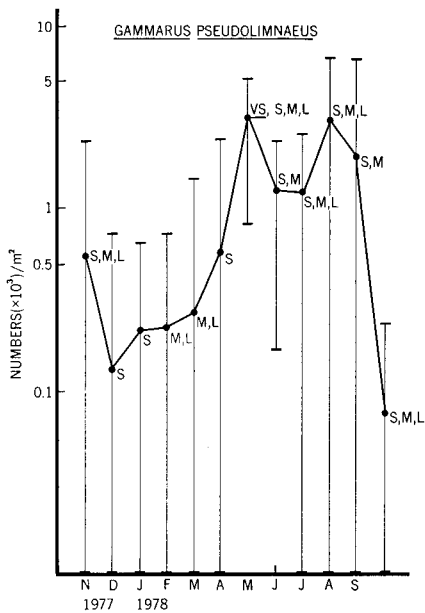


Fig. 11. Annual recolonization curve for *Gammarus pseudolimnaeus* (animal size is approximated by the categories — very small, small, medium and large).

Numbers of colonizing *Gammarus pseudolimnaeus* BOUSFIELD were generally low in the winter and high in the summer (Fig. 11). Apart from a large influx of very small animals in May, no size class dominated either winter or summer collections. The curve for this species shows it to be the highest clumper of all the taxa studied. This could well be due to its high mobility and tendency to cluster around a preferred food source.

Discussion

The animals moving onto the baskets came from various directions in the stream (upstream, downstream, laterally, from within the substrate or through oviposition — see WILLIAMS & HYNES, 1976). However, downstream drift has been shown to be the major contributor in permanent streams (e.g., 82%, TOWNSEND & HILDREW, 1976; 41%, WILLIAMS & HYNES, 1976), although the situation may be very different in streams of a temporary nature (WILLIAMS, 1977). Few studies exist in which directional movements, other than drift, have been shown to be under the control of environmental parameters (e.g., BISHOP & HYNES, 1969).

Clearly, the annual colonization pattern of the total benthos in the upper, east branch of Duffin Creek is related to water temperature. In a warm water stream in Illinois, LARIMORE (1972) showed a relationship between the pattern of drift and the season. He found an increase in the abundance of organisms drifting during the spring and summer, and a gradual decline in the late fall to minimum values in the winter. Control of this pattern was attributed to light. In the present study, the total monthly amount of incident radiation did not correlate, either positively or negatively, with the numbers of animals moving onto the baskets ($r = 0.49$). Other authors have shown that temperature controls the drift of some taxa, with different species reacting differently at different times of the year. MÜLLER (1966), for example, showed that an increase in temperature always increased the drifting of *Gammarus pulex*, particularly during its summer breeding season. *Baëtis vernus* also drifted most in midsummer. MADSEN (1968) indicated that the resettling behaviour in *Heptagenia* was temperature related but his interpretations of the results seem inconsistent. OLSSON & SÖDERSTRÖM (1978) recorded a mass migration of nymphs of *Parameletus chelifera* into a temporary tributary of the Swedish River Vindelälven in May. Higher temperatures and more plentiful food in the tributary may have been responsible (see also WILLIAMS & HYNES, 1977). There are, however, examples of inverse relationships between movement and temperature. The migration of nymphs of *Heptagenia interpunctata* away from lake shores in the U.S.A. during autumn was thought to be due to falling water temperature (WODSEDALEK, 1912). KELLER (1975), con-

versely, found that an increase in temperature caused a decrease in the drift of *Ecdyonurus venosus*.

The fact that the total numbers colonizing the baskets did not correlate with current speed strongly suggests that the animals were not being passively carried onto the substrates (see "catastrophic" and "constant" drift categories of WATERS, 1965), but were moving onto them through activity under their own control ("behavioural" category). A straightforward relationship between the numbers of animals drifting and flow was evident in a study by LOGAN (1963) and, at times, in LARIMORE's (1972) study. In addition, CLIFFORD (1972) found that the total daily drift across an intermittent section of the Bigoray River, Alberta varied directly with flow. TOWNSEND & HILDREW (1976), none-the-less, found high rates of movement onto artificial substrates even during low flow conditions (< 5 cm/s) in an english stream. Complete cessation of the current, in the case of the stonefly *Brachyptera risi*, resulted in most of the population entering the water column (MADSEN, 1959). The tendency for some animals to drift more as current decreases, and, presumably, water depth decreases, may have accounted for the negative correlation between numbers moving onto the baskets and water depth obtained in Duffin Creek.

The colonization patterns for some individual taxa show distinct discontinuities which suggests considerably variation in seasonal mobility (see also ULFSTRAND et al., 1974). Quite a few species were totally missing from all three baskets in some months. *Dolophilodes distinctus*, for example, did not move onto the baskets in December or February, and its density on them in the other winter months was low — although it was present in the stream as third and fourth instars. It is likely that low water temperature suppressed activity of most of the population at this time rather than these later instars being inherently quiescent, as during the summer months all instars moved onto the baskets in large numbers. Third instar larvae of *Cricotopus/Orthocladius* were also relatively inactive during the winter, although in March, before any significant rise in water temperature, more larvae colonized the baskets. The absence of larvae in July and August was probably the result of latent egg-hatching, as first instars immediately colonized when they first appeared in September.

Many other species showed mass colonization by first instars, for example, *E. subvaria* in July, *E. deficiens* in May and July, *Polypedilum* in July, nematodes in July and *G. pseudolimnaeus* in May. Both species of *Rheotanytarsus*, in contrast, were represented by low densities of their first instar larvae during June. MÜLLER (1973) observed an increase in the drift of early instar larvae, primarily baëtids and simuliids, and termed this phenomenon "distributional drift", a means by which a superfluity of young in headwater regions regulates and maintains the population through time-

regulated downstream migration. Other workers have supported this theory (e.g., TOWNSEND & HILDREW, 1976 and WILLIAMS, 1977). Exceptions to the process may be due to peculiarities in a species' life cycle.

The Duffin Creek study also provides examples of increased mobility in later instars. Very large numbers of final instar larvae of *Polypedilum* sp. 2, for example, colonized the substrates in July, and peak numbers of predominantly fourth instar larvae of *Cricotopus/Orthocladius* occurred in June. These may represent pre-emergent migrations. Downstream migrations shortly before pupation or emergence are known for species of Plecoptera, Ephemeroptera and Simuliidae (MACAN, 1957, 1964; DORRIS & COPELAND, 1962; MÜLLER, 1966). They may be the results of changes in behaviour (HYNES, 1970). KELLER (1975), on the other hand, found that a drift minimum occurred in the final larval instar of *Ecdyonurus venosus* and attributed this to a "pseudo-pupal" stage. Other authors have found drift maxima associated with other stages in the life cycle. ELLIOTT (1967), for example, found maxima to coincide with periods of maximum growth for certain Plecoptera and Ephemeroptera, while CIBOROWSKI (1979) observed that the nymphs of *E. subvaria* drifted more when they were not growing.

Dependence of propensity to move on an animal's growth implicates food, both in quantity and quality, as a causal agent. KELLER (1975) cited scarcity of food as a drift inducing factor, and BOHLE (1978) found that food supply caused lack of drift in larvae of *Baëtis rhodani*. TOWNSEND & HILDREW (1976) suggested that discontinuities seen in the patterns of colonization of certain species could be explained in terms of variations in arrival and departure rates which, in turn, are influenced by a build-up of detritus and microflora (see also WILLIAMS et al., 1977). Seasonal abundance of different food types, e.g., FPOM, CPOM and periphyton, may therefore, in narrow range feeders, control periods of intensive growth and/or quiescence. In this way, food and its availability may control the life cycle of a species (ULFSTRAND, 1968), and may also control set patterns of migration within that life cycle. This relationship may be most noticeable in constant temperature springs (THORUP, 1963). In Duffin Creek, however, food available for detritivores does not appear to be limiting (WILLIAMS, 1980) and this may account for the lack of correlation between numbers moving onto the baskets and organic matter. The latter may also be responsible for the wide variations in numbers between the baskets, as BOHLE (1978) found that abundant food supply caused local concentrations (clumping) in a population of *B. rhodani*, while a nearly uniform distribution of animals resulted on its depletion. Furthermore, this may explain why the deviations around the mean values of animals in Fig. 4 were greater from December to March, a time when the ratio of numbers of animals to amount of detri-

tus in each basket was relatively lower (resulting in greater clumping) than during April to November.

Conclusion

Streams are dynamic systems and the animals that live in them reflect this in that they move around a great deal. Much of this movement is behavioural although stimuli from the animals' environment may initiate or arrest it. In this study, water temperature and depth are shown to be important, although other studies have implicated different parameters. Such parameters may act singly or in combination and the response that they elicit may differ from species to species and perhaps from stream to stream. These facts, together with the indication that some species show discontinuities in their seasonal mobility suggest that caution should be applied in stream studies where artificial substrate techniques are used to collect information such as species composition and the effects of pollutants, especially where these inventories are only made once or twice a year.

Acknowledgements

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Summary

The recolonization patterns of members of a natural stream community were studied over one year using baskets of substrate implanted on a riffle. The size composition of inorganic sediment collected by the substrates was found to change over the year, with larger particles settling after the spring runoff and particles less than 125 μm settling in the summer. Amounts of FPOM and CPOM settling in the substrates were measured but these did not correlate with the numbers of animals colonizing.

Relatively low numbers of animals colonized the substrates in the winter months (December—March) compared with the summer months (June—September). This is thought to be primarily the effect of temperature acting on the animals' behaviour. Species diversity was also lower on the substrates in winter. There was a negative correlation between numbers of animals moving onto the substrates each month and water depth. Recolonization curves for individual taxa were different but most could be categorized into three similar patterns. Some curves were unique. Distinct discontinuities in the curves of some species suggest variation in seasonal mobility and this may be associated with particular stages in the life cycle. The mass colonization by first instar larvae of many species supports the theory of "distributional drift". Some insect species may exhibit a pre-emergence migration.

A superabundance of food in the form of detritus may have resulted in the clumped distributions seen in many of the colonizing species. The relevance of these findings to interpretation of data collected by artificial substrate techniques is discussed.

Zusammenfassung

Die Wiederansiedlungsmuster von Mitgliedern einer natürlichen Flußgemeinschaft wurden ein Jahr lang mit Hilfe von Körben mit Substraten, die in eine Stromschnelle eingepflanzt wurden, beobachtet. Die Partikelgröße der anorganischen Ablagerungen, die von den Substraten gesammelt wurden, variierte während des Jahres, indem sich größere Partikel nach dem Frühlingsabfluß und Partikel unter $125\ \mu\text{m}$ Größe im Sommer absetzten (Abb. 2). Die Mengen von feiner und gröberer partikulärer organischer Substanz, die sich in den Substraten absetzten, wurden gemessen, aber diese Mengen ließen sich nicht mit der Zahl von sich ansiedelnden Tieren korrelieren (Abb. 3). Im Vergleich mit den Sommermonaten (Juni bis September) siedelte sich in den Wintermonaten (Dezember bis März) eine relativ niedrige Zahl von Tieren in den Substraten an. Dies ist vermutlich primär als Auswirkung der Temperatur auf das Verhalten der Tiere zu verstehen. Die Arten-Verschiedenheit auf den Substraten war im Winter auch geringer (Abb. 4 und 5). Es gab eine negative Korrelation zwischen der Zahl der Tiere, die sich jeden Monat auf den Substraten ansiedelten, und der Wassertiefe. Die Wiederansiedlungskurven für einzelne Taxa waren verschieden, aber die meisten ließen sich unter drei ähnlichen Mustern kategorisieren (Abb. 6 bis 8). Einige Kurven waren einzigartig (Abb. 9 bis 11). Besondere Diskontinuitäten in den Kurven einiger Arten lassen eine Variation in der jahreszeitlichen Beweglichkeit vermuten, und dies kann mit bestimmten Phasen des Lebenszyklus zusammenhängen. Die Massenansiedlung der Erstlarven vieler Arten unterstützt die Theorie einer Ausbreitungsdrift (Abb. 7, 8 und 11). Einige Insektenarten können eine Wanderung vor ihrer Emergenz aufweisen (Abb. 8 und 9). Ein Überfluß an Nahrung in Form von Detritus kann zu der klumpenhaften Verteilung geführt haben, die bei vielen angesiedelten Arten zu sehen war (Abb. 11). Die Relevanz dieser Ergebnisse für die Interpretation von Meßwerten, die von künstlichen Substrattechniken gewonnen werden, wird diskutiert.

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