Colonisation patterns of mayfly nymphs (Ephemeroptera) on implanted substrate trays of different size

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Abstract

Colonisation by nymphs of eight mayfly species was monitored in a small stream using implanted natural substrate trays of different area during a seven day period.

All species colonised the trays, but to various degrees. Downstream drift and directed or random crawling over the substrate contributed equally to colonisation of the implanted substrates.

The area of the implanted substrate trays had profound effects on the diversity, density and size frequency distributions of the colonising assemblage. Density declined, but overall diversity and mean size of most mayfly species increased as tray size increased.

The influence of implanted substrate tray area on the above parameters indicates potential problems in the use of colonisation studies to examine the composition and dynamics of lotic invertebrate assemblages. This is especially so given the lack of standardisation of colonisation samplers between such studies.

Introduction

Colonisation studies are becoming an increasingly popular experimental methodology for examining the composition, distribution and dynamics of lotic invertebrate assemblages. They make use of the extraordinary motility of lotic invertebrate populations to allow invasion of the clean and/or implanted substrates to mimic patterns and processes in natural assemblages (e.g. Ulfstrand, Nilsson & Stergar, 1974; Townsend & Hildrew, 1976; Bird & Hynes, 1981; Rosenburg & Resh, 1982; Benzie, 1984; Reynolds & Hunter, 1984). Invertebrate movements involved in colonisation and redistribution are normally attributed to one of four possible mechanisms; downstream drift, aerial sources, upstream and vertically directed movements (Williams & Hynes, 1977), but random lateral movements can contribute a fifth mechanism, especially when new areas, such as implanted substrates, become available within populated habitats. Downstream drift is usually considered to be the most important colonisation/redistribution mechanism (Townsend & Hildrew, 1976; Bird & Hynes, 1981; Graesser & Lake, 1984), although the propensity to drift is not the same in all species (Chaston, 1972; Turcotte & Harper, 1982; Köhler, 1983; Allan, 1984). Other studies have demonstrated that movement on, or in, the substrate can also contribute significantly to overall redistribution of benthos (e.g. Elliott, 1971; Butler & Hobbs, 1982; Benzie, 1984). Vertical movement is considered to play very little part in benthic redistribution, as is aerial

colonisation during short-term studies (although the latter must be important in colonisation of new areas over time).

Despite the increasing use of colonisation samplers, there is little or no standardisation in the technique. The nature of the colonisation substrate is likely to have some effect on the composition of the colonising fauna, and this aspect has been examined in a number of studies (e.g. Mason, Weber, Lewis and Julian, 1973; Allan, 1975; McConville, 1975; Hall, 1982; Morin, 1985). Taxa also colonise at different rates depending both on their mode of movement and on their propensity to move. Time allowed for colonisation is, therefore, an important and recognised parameter, (e.g. Allan, 1975; Cover & Harrel, 1979) much dependent on the nature and flow regime of the system. However, large variation in the period of exposure of colonisation samplers is found in the literature. Less obvious are the problems associated with the size of the individual colonisation samplers on both composition and abundance of the colonising fauna. It is to this problem that the present work is addressed, specifically examining the effect of size of implanted colonisation samplers on the composition, density and size structure of colonisers from a specific group of invertebrates, the mayflies (Ephemeroptera).

Mayfly nymphs show the full spectrum of recolonisation/redistribution propensity. They form a major part of the drift in most lotic systems (Elliott, 1967; Bird & Hynes, 1981) although different species show different propensities to drift (e.g. Anderson & Lemkuhl, 1968). There are also conflicting reports as to the likelihood of different size classes of a species to drift (e.g. Anderson & Lemkuhl, 1968; Bishop & Hynes, 1969). Mayfly nymphs are also reported to move upstream (e.g. Elliott, 1971; Brown & Brown, 1984) and to show random movements on and within the substrate (e.g. Elliott, 1971; Köhler, 1983). Mayflies thus appear to represent a useful group on which to examine the effect of colonisation sampler size on colonisation/redistribution patterns of the benthos.

Methods

The study site was a 10 m stretch of riffle just upstream of a pool, situated in the River Blackwater, a small tributary of the River Bandon, Co. Cork, Ireland (O.S. W290565), described in detail elsewhere (Cambell, 1985). During the present study, depth varied from 19.5 to 33 cm ($x = 25.9 \pm 7.15$, 95% CL), width was 6 m and current speed ranged between 0.2 and 0.5 m s^{-1} (average discharge 0.58 m^{-3} S^{-1}). The substrate was mainly coarse gravel with small pebbles and stones up to a maximum length of 10 cm. The experiment was conducted during early summer.

Colonisation

Colonisation was studied using implanted perspex trays of different sizes containing natural substrate taken directly from the stream site. The square trays were 3 cm deep, constructed from 3 mm thick perspex sheeting and strips glued together and strengthened with thin rectangular perspex blocks between the sides and base of the trays. (see Table 1 for tray size classes and number of replicates). Impermeable bases reduced possible invertebrate losses on removal of the tray from the stream-bed, but prevented vertical migration into the clean area. Such colonisation samplers may increase siltation (Welton, Cooling & Ladle, 1982), but are widely used (e.g. Hildebrand, 1974; Ulfstrand *et al.*, 1974; Townsend and Hildrew, 1976). They yield less variable density estimates than average for artificial samplers and direct natural substrate samplers of stream benthos (Morin, 1985). The substrate for the implanted trays was dug out of the stream-bed from each tray site (see below) and invertebrates were removed by elutriation on site. The entire quantity of cleaned substrate was thoroughly mixed and placed in the perspex trays. Detailed checks on several substrate samples returned to the laboratory revealed 100% removal of mayfly nymphs.

Filled trays were sited randomly within a 10 × 6 m grid in the riffle, laid flush with the stream bottom, and left for 7 days. Careful removal of trays with 0.5 mm mesh nets held

Table 1. Summary of mayfly density data from colonisation trays. Derived mean density calculated from transformed data (log x + 1) with confidence limits and corrected to No's per m². S – Surber samples (n = 8), A–F colonisation trays (dimensions (cms) and area (m²)). A – 6 × 6 cm (0.0036 m²); B – 12 × 12 cm² (0.0144 m²); C – 18 × 18 cm² (0.0324 m²) D – 24 × 24 cm (0.0576 m²); E – 30 × 30 cm (0.09 m²); F – 45 × 45 cm (0.203 m²).

	Tray Size (numbers of implanted/recovered replicates in parentheses)						
	S	A (8/7)	B (6/6)	C (6/5)	D (6/4)	E (6/5)	F (3/2)
Baetis rhodani	827.5 $\overset{\times}{\div}$ 2.18	2358.1 $\overset{\times}{\div}$ 3.07	1902.77 $\overset{\times}{\div}$ 3.8	688.23 $\overset{\times}{\div}$ 1.5	664.23 $\overset{\times}{\div}$ 1.5	420 $\overset{\times}{\div}$ 1.87	222.2*
B. muticus	27.61 $\overset{\times}{\div}$ 1.79	0	72.22 $\overset{\times}{\div}$ 1.73	59.94 $\overset{\times}{\div}$ 2.1	39.23 $\overset{\times}{\div}$ 2.9	98.55 $\overset{\times}{\div}$ 2.5	51.85*
Ephemerella ignita	1070 $\overset{\times}{\div}$ 1.4	2608.4 $\overset{\times}{\div}$ 1.79	1294.28 $\overset{\times}{\div}$ 1.3	724.38 $\overset{\times}{\div}$ 1.79	742.5 $\overset{\times}{\div}$ 1.38	689 $\overset{\times}{\div}$ 1.55	441.9*
Caenis rivolorum	207.67 $\overset{\times}{\div}$ 1.27	205.5 $\overset{\times}{\div}$ 1.5	96.52 $\overset{\times}{\div}$ 1.49	51.42 $\overset{\times}{\div}$ 1.2	124.13 $\overset{\times}{\div}$ 1.87	88.33 $\overset{\times}{\div}$ 1.6	51.85*
Ecdyonurus spp.	80.8 $\overset{\times}{\div}$ 2.4	80.55 $\overset{\times}{\div}$ 1.36	22.77 $\overset{\times}{\div}$ 1.6	0	26.56 $\overset{\times}{\div}$ 2.4	78.11 $\overset{\times}{\div}$ 3.8	12.34*
Heptagenia sulphurea	19.84 $\overset{\times}{\div}$ 1.89	0	0	12.5 $\overset{\times}{\div}$ 1.83	9.2 $\overset{\times}{\div}$ 1.88	16.55 $\overset{\times}{\div}$ 1.8	2.47*

* Arithmetic average due to low number of replicates.

immediately downstream ensured minimal loss of colonising fauna, but a few trays (from different tray size classes) were abandoned due to silting (see Table 1). All tray contents were placed in bags, the fauna preserved with alcohol and samples returned to the laboratory for analysis. Simultaneous placement and removal of trays ensured that all were exposed to similar fluctuations in environmental conditions and that animals collected were from the same sampling population (c.f. Ciborowski and Clifford, 1984). Random Surber samples of benthos (0.0625 m^{-2}, mesh size 0.5 mm, n = 8) were taken to provide background data of animal size distributions and density against which the colonisation and drift samples could be compared.

Drift
Drift sampling was carried out using pairs of nets (100 mm high, 140 mm wide × 1 m long, of 0.5 mm mesh) set in metal stacks to sample the top 100 mm of the water column and a lower 100 mm to within 25 mm of the bottom (Campbell, 1985). Five stacks were placed across the stream. Night samples were of 4 hours duration, starting one hour before sunset, and taken on the first and last nights of the study. Natural drift monitored during day time hours was negligible.

Analysis
Invertebrates were removes from the sample substrate by elutriation through a 0.5 mm mesh sieve and all mayflies were hand sorted and preserved. Nymphs were identified to species, counted, and body lengths from the front of the head to the posterior edge of the abdomen were measured to the nearest 0.5 mm. Damaged nymphs were not measured.

Mayfly densities were calculated from transformed data ($\log x \pm 1$) and these data compared using 't'-tests. Comparisons of body length frequency distributions between surber, colonisation tray and where appropriate, drift samples where made for each species using χ^2 contingency tests. Mayfly species diversity and equitability were calculated using the Shannon-Wiener function.

Results

Eight species of mayfly were collected in benthic samples during the study and identified mainly using Macan (1979). Giller (1986) was used to identify individuals from the two *Baetis* species.

Baetis rhodani (Pict.), *Ephemerella ignita* (Poda) and *Caenis rivulorum* Etn. were the most common. *Baetis muticus* (Linn.), *Ecdyonurus dispar* (Curt.) and *E. venosus* (Fabr.) were less common and data on the latter two species were pooled to allow statistical analyses. *Heptagenia sulphurea* (Mill) was quite rare and *Rithrogena semicolorata* (Curt.) was too rare for inclusion in the data set. All eight species colonised implanted substrate trays, but to various degrees. Tables 1 and 2 present a summary of density and size of mayfly nymphs from Surber (control) samples and colonisation trays. Total absolute numbers of nymphs in the various sized trays are given in Table 3. A summary of statistical comparisons is given below.

Species Density
For the two commonest species, *B. rhodani* and *E. ignita*, density tended to decrease as colonisation tray size increased, *(B. rhodani* – A = B ≠ D = E, P < 0.05; *E. ignita* – A ≠ B ≠ D = C = E, P < 0.02). The control density lay between the smaller tray (A and B) and larger tray (C–F) densities.

Numbers of *B. muticus*, *C. rivulorum* and *Ecdyonurus* spp. colonising substrate trays were low, reflecting, in part, their low natural density. *B. muticus* did not colonise the smallest trays, but achieved a greater density than the control in the other sized trays (P < 0.05). Highest densities of *C. rivulorum* and *Ecdyonurus* spp. were found in control and the smallest tray samples, but no general pattern was apparent, *(C. rivulorum* – S = A ≠ D = B = E = C; P < 0.02; *Ecdyonurus* – S = A = E ≠ D = B ≠ C: P < 0.02).

The numbers of *H. sulphurea* colonising the substrate trays were very low and none were found in the smallest trays.

Drift
Natural drift comprised almost entirely of baetid nymphs, over 90% of the larger individuals of

Table 2. Summary of mayfly size data from colonisation trays. Mean body length based on arithmetic data with ± 1 SD. S – Surber samples, A–F colonisation trays (number of replictes and tray size dimensions as in Table 1). n = number of mayflies measured.

	Tray size						
	S	A	B	C	D	E	F
Baetis rhodani	3.216 ± 1.236 n – 384	2.611 ± 1.49 n – 50	2.6 ± 1.56 n – 161	2.53 ± 1.54 n – 85	4.37 ± 1.57 n – 126	4.036 ± 1.6 n – 108	4.765 ± 1.52 n – 71
B. muticus	5.063 ± 1.36 n – 11	–	5.08 ± 0.925 n – 5	4.46 ± 1.42 n – 8	4.985 ± 1.16 n – 9	5.44 ± 0.93 n – 20	5.646 ± 0.93 n – 13
Ephemeralla ignita	3.947 ± 2.53 n – 460	4.04 ± 1.71 n – 53	4.16 ± 1.72 n – 119	4.287 ± 1.98 n – 107	4.47 ± 1.71 n – 164	4.46 ± 1.71 n – 256	4.9 ± 1.63 n – 177
Caenis rivulorum	3.554 ± 0.64 n – 105	3.46 ± 0.47 n – 5	3.8 ± 0.614 n – 8	4.18 ± 1.014 n – 8	3.46 ± 0.64 n – 31	3.44 ± 0.94 n – 33	3.58 ± 0.505 n – 20
Ecdyonurus spp.	4.53 ± 0.77 n – 35	Combined Trays 8.42 ± 0.817 n – 40					
Heptagenia sulphurea	4.68 ± 2.18 n – 10	Combined Trays 5.72 ± 2.02 n – 11					

Table 3. Proportional representation and diversity of mayfly nymphs in the benthos (S) and colonising substrate trays (A–F). Diversity was calculated using the Shannon-Wiener function (H′ = $\sum^{S_T} p_i \log_e p_i$, where p_i is the proportion of individuals in the ith species and S_T the total species), and equitability (E) was derived as the ratio $\dfrac{H}{Hmax}$ (H max = $\log_e S_T$). Values in brackets are the cumulative absolute number of nymphs of each species in the various sized trays and benthic samples.

Species	Treatment (n = number of replicates)						
	S (n = 8)	A (n = 7)	B (n = 6)	C (n = 5)	D (n = 4)	E (n = 5)	F (n = 2)
Baetis rhodani	35.65 (384)	41.17 (49)	58.5 (179)	43.33 (104)	41.41 (152)	30.06 (181)	28.4 (90)
B. muticus	1.2 (13)	0	1.96 (6)	4.17 (10)	2.18 (8)	6.64 (40)	6.62 (21)
Ephemerella ignita	49.11 (529)	52.94 (63)	36.27 (111)	48.33 (116)	46.32 (170)	50.8 (306)	56.46 (179)
Caenis rivulorum	9.56 (103)	4.2 (5)	2.61 (8)	3.33 (8)	7.63 (28)	6.48 (39)	6.62 (21)
Ecdyonurus dispar	2.41 (26)	0.84 (1)	0.65 (2)	0	1.09 (4)	2.32 (14)	0.31 (1)
Ecdyonurus venosus	0.83 (9)	0.84 (1)	0	0	0.54 (2)	2.5 (15)	1.26 (4)
Heptagenia sulphurea	0.93 (10)	0	0	0.83 (2)	0.54 (2)	1.16 (7)	0.31 (1)
Rhithrogena semicolorata	0.28 (3)	0	0	0	0.27 (1)	0	0
Diversity H′	1.184	0.915	0.886	0.99	1.123	1.294	1.131
Equitability E	0.569	0.44	0.426	0.48	0.54	0.622	0.543

which were *B. rhodani*. Of the other mayfly species only *C. rivulorum* were found in drift samples, but in very small numbers (1 to 2.5% of baetid numbers). Size frequency data for *B. rhodani* nymphs in benthic and drift samples are shown in Fig. 1. There was a significant difference between these distributions (χ^2 p < 0.001), due largely to under-representation of larger nymphs in the drift.

Size Frequency Distributions

All replicate data were pooled for statistical comparisons between size frequency distributions.

Whilst the large number of statistical comparisons increases the likelihood of Type II errors (a comparison deemed significantly different but which may be due to chance), the high levels of significance found substantially reduced this possibility, (in 80% of comparisons, p < 0.001). For *B. rhodani* (Fig. 2, Table 2) the overall treatment contingency test was significant (p < 0.001) and only three between-treatment comparisons were not (A–B, C–E, D–E). Smaller nymphs were the predominant colonisers of smaller trays (A and B), but larger nymphs became proportionately more important as tray size increased. Size dis-
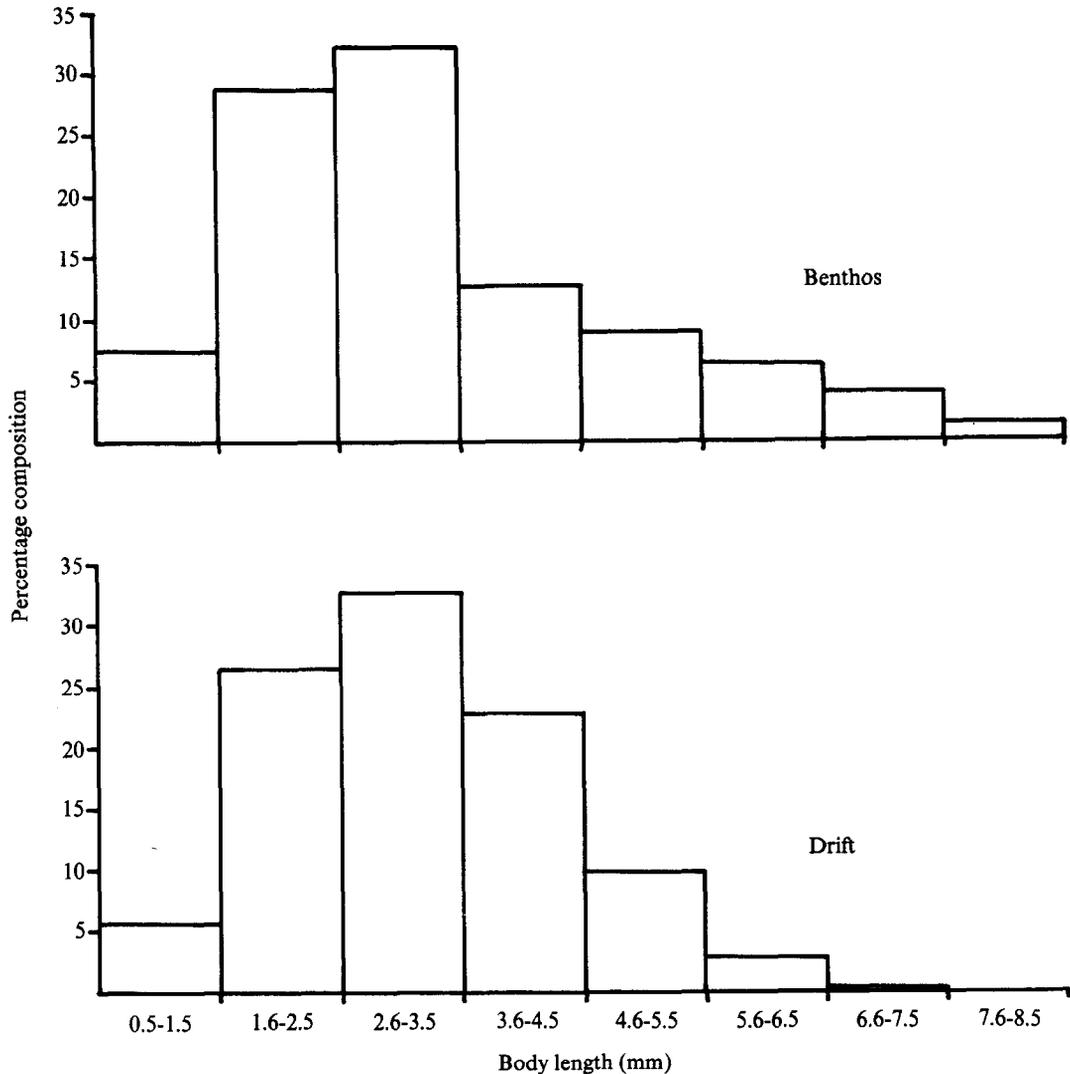
Fig. 1. Histograms showing the size frequency distribution data (1 mm size classes) for *Baetis rhodani* nymphs in drift and benthic samples. (χ^2 contingency comparison: $\chi^2 = 4.546$, N.S.)

tributions of *B. rhodani* in drift and control samples lay between the two extremes. The overall treatment contingency test was also significant ($p < 0.001$) in *E. ignita*. Six between-treatment comparisons were insignificant (A – S,B,C,D and B–E) but the same trend was apparent, with an increasing proportion of larger nymphs colonising trays as tray size increased (Fig. 3, Table 2). Nymphs in benthic samples showed the smallest mean size although the size distribution differs significantly only from that of three largest tray samples (D–F, $p < 0.001$). Low numbers of

C. rivulorum were found in all but the three largest sets of trays, and no differences between size frequency distributions of colonising and benthic nymphs were found (Fig. 4).

The size frequency data for *Ecdyonurus* nymphs from all trays were pooled due to low numbers (Fig. 4) and clearly demonstrated that a significantly greater proportion of larger nymphs colonised the trays than were present in the benthos ($P < 0.001$). Insufficient data were available for analysis of either *B. muticus* or *H. sulphurea* colonisation.

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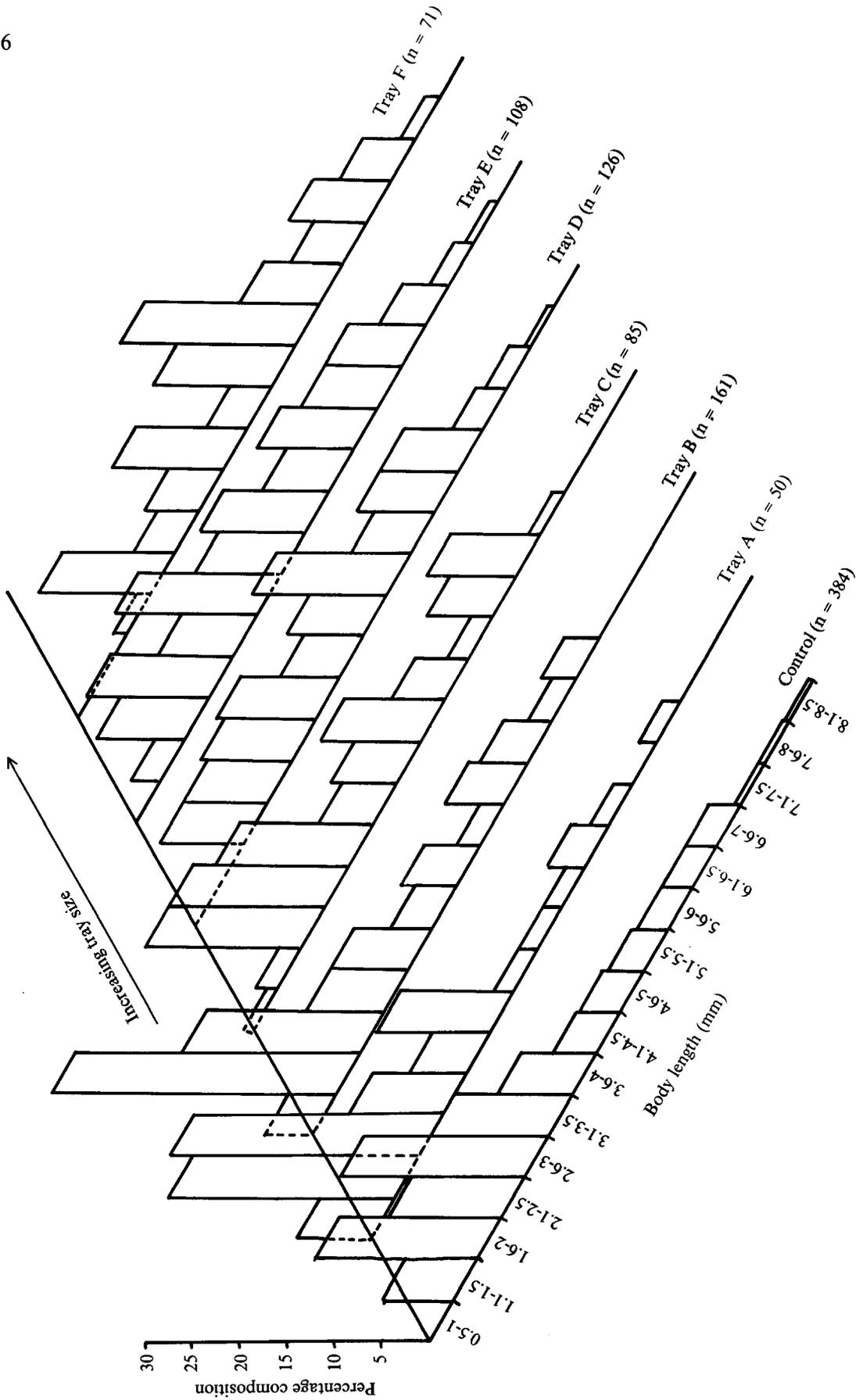
Fig. 2. Histograms showing the size frequency distribution data (0.5 mm size classes) for *Baetis rhodani* nymphs in benthic (control) and colonisation tray samples. Tray sizes are given in Table 1. (n = sample size).

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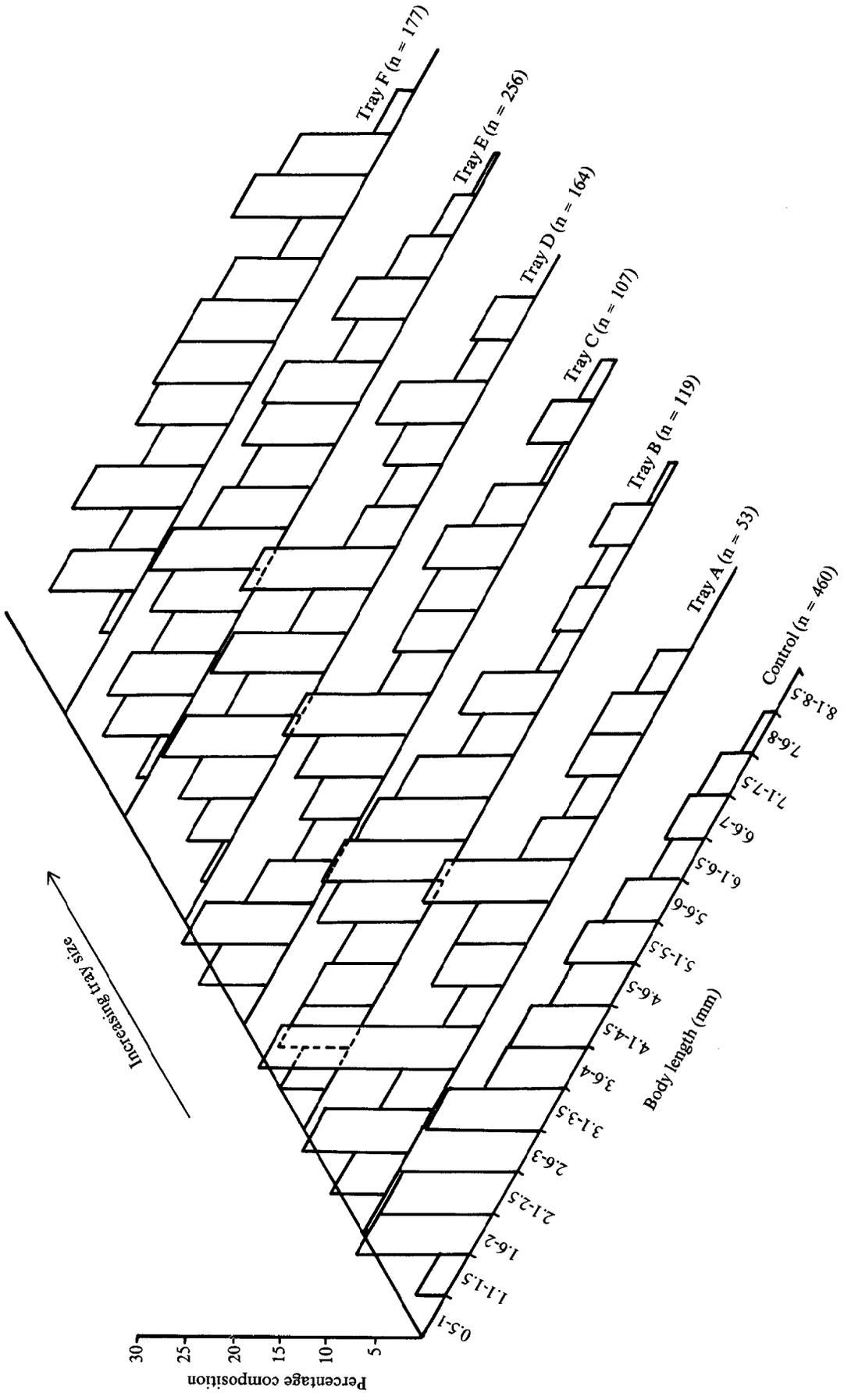
Fig. 3. Histograms showing the size frequency distribution data (0.5 mm size classes) for *Ephemerella ignita* nymphs in benthic and colonisation try samples. Tray sizes are given in Table 1. (n = sample size).
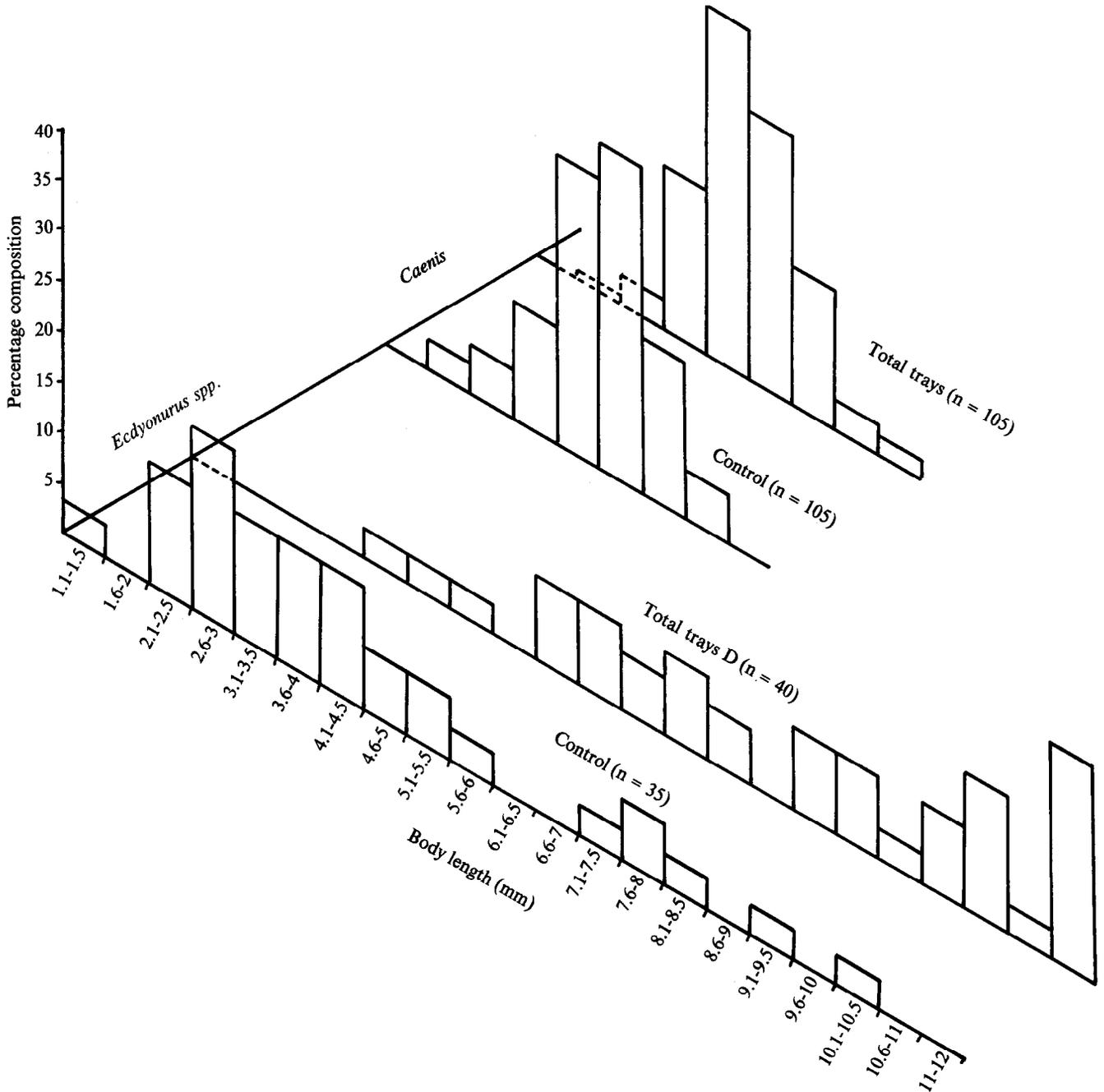
Fig. 4. Histograms showing the size frequency distribution data (0.5 mm size classes) for *Ecdyonurus* spp. and *Caenis rivulorum* nymphs in benthic and pooled colonisation tray samples. (n = sample size).

Diversity

Whilst most substrate trays were colonised by all species, differences in diversity between tray sizes were evident. Diversity and equitability were lowest in the smallest trays, whereas control levels were achieved or surpassed in the larger trays (Table 3). As a proportion of total mayflies, *B. muticus* exceeded control levels in all but the

smallest colonisation trays, and *B. rhodani* exceeded control levels in the four smaller sized trays. The proportional contribution of both *C. rivulorum* and *Ecdyonurus* spp. colonising trays was generally lower than in controls, but no pattern was shown by *E. ignita*.

Discussion

Colonisation

The rates of colonisation and recolonisation of streams benthos depend on the taxa (Ciborowski & Clifford, 1984), but are also related to the extent of the uncolonised area and its proximity to the source of colonisers. Thus new areas require more than a year to reach equilibrium (Minshall, Andrews & Manuel-Faler, 1983). Severely denuded or stressed systems may require between 70 and 150 days (Gore, 1982), whereas rapid colonisation of artificial or implanted substrates can occur within time periods ranging from 1–4 days (Allan, 1975; Ciborowski & Clifford, 1984), to 2–4 weeks (Ulfstrand *et al.*, 1974; Townsend & Hildrew, 1976; Köhler, 1983 & Benzie, 1984). In the present study, relatively high abundances were reached compared to natural densities, given the short exposure period of the substrate trays. This may be related to the collector/scraper trophic status of the mayfly species (Cummins, 1983), as members of these trophic groups are reported to be amongst the first to arrive and attain densities and diversities comparable with control areas (Gore, 1982).

Nymphs were able to colonise either through drift or by directed or random movements over the substrate. *Baetis* dominated the drift and other species were effectively absent (see also Bailey, 1965; Anderson & Lemkuhl, 1968; Neveu, 1980; Bird & Hynes, 1981; Graesser & Lake, 1984). This can largely be related to morphology and behaviour, so that one can, for example, classify mayfly into rare passive drifters (e.g. *Ecdyonurus* spp, *H. sulphurea*, *R. semicolorata*), frequent passive drifters (e.g. *E. ignita*, *C. rivulorum*) and active drifters (e.g. *Baetis* spp.). Active swimmers usually reach an empty area first (Gore, 1982) and their densities can quickly reach or even exceed natural benthic densities (e.g. for *Baetis*, Ulfstrand *et al.*, 1976; Ciborowski & Clifford, 1984). Thus drift is usually considered to initially provide the largest source of early colonists. Species then start to arrive through other processes (Williams & Hynes, 1977). When the distances between empty and populated substrates are small (as in the situation for implanted substrates), these other mechanisms may be as important in the initial stages of colonisation, and in some cases, directed and random movements over the substrate match movements via drift (e.g Butler & Hobbs, 1982; Benzie, 1984). The combined importance of drift and crawling to colonisation was clearly shown in the present study by the similarly high levels of colonisation by the numerically dominant drifting *Baetis* and crawling *Ephemerella* nymphs. A lower level of colonisation, and hence activity, is shown by *C. rivulorum* and even lower levels of movement are indicated by colonisation of the two species of *Ecdyonurus*.

Diversity

Tray size affected the ensuing diversity of the colonising assemblages as might have been expected given the widespread phenomenon of the species-area relationship (see Allan, 1975). The larger tray assemblages matched the natural benthic diversity although the latter was based on a smaller sample area. These differences in tray size highlight a possible problem in the widespread use of unstandarised implanted substrates for analysis of benthic invertebrate assemblages.

Density

Colonisation is likely to be due to random effects, either chance landing from drift or chance wandering from neighbouring areas. Whilst it is possible only to speculate on whether an equilibrium has been reached during the experimental period, the numbers colonising the substrate trays must represent some dynamic balance between departures and arrivals. From the present study, it is evident that density of the more common species declined as tray size increased. A small area obviously offers a smaller 'target' for chance

arrival and departure than a larger area, but on the other hand, offers relatively more edge per unit area across which colonisation can take place. Large areas may also require longer periods of time to equilibrate with the surrounding benthos than smaller areas, with respect to density (N.B. the presence of one individual on a small tray has a much more pronounced effect on the calculated density (no. per m²) than is the case for large trays). The trays could also be creating an 'artificial' environment, e.g. altering the pattern of currents, influencing the exchange of materials with the surrounding environment, initially presenting an area free of other animals etc. These factors will all vary with size of the substrate tray and hence could influence colonisation in different ways. The present data however are insufficient to test between these various possibilities.

Size
Based on the knowledge of mayfly life history strategies (Macan, 1979; Clifford, 1982) an almost complete size range of nymphs was available for colonisation in this study (Figs. 2–4). However significant size differences were evident within the species colonising the different sized substrate trays. In both *E. ignita* and *B. rhodani* and to a lesser extent, *B. muticus*, there was a positive relationship between tray size and average size of colonists. For *Ecdyonurus* spp. and to a lesser extent *H. sulphurea*, significantly larger individuals tended to colonise the trays. No obvious explanation lends itself to these findings.

The Use of Implanted Substrates
The increasing popularity of colonisation studies in lotic systems is due largely to the fact that colonisation samplers offer a number of advantages over direct sampling (Cover & Harrel, 1978; Rosenburg & Resh, 1982). These include easier sampling in difficult and patchy environments; the ability to obtain qualitatively comparable data from environments from which it may be impossible to obtain samples with conventional devices; a higher level of precision (reduced variability) may be obtained than with other sampling

devices, and more control over study design may be possible. However, difficulties are apparent. As mentioned earlier, differential colonisation rates by taxa and different time periods for colonisation are important and recognised parameters affecting the efficiency of colonisation samplers. Less obvious are the problems associated with the size of colonisation samplers. Colonisation samplers are used to study the dynamics, distribution, and structure of benthic invertebrate assemblages. The major indices of such parameters are diversity, density and size frequency distributions, and all three were affected by the size of the sampler in this study. Compared to benthic surber samples, density estimates declined with increasing colonisation sampler area, whereas mean size of nymphs increased in most species. The expected species-area relationship was apparent, but benthic diversity was reached only in the largest tray sizes during the colonisation period used in the study. Whatever the biological or physical reasons behind these patterns, their occurrence raises questions about the efficiency and usefulness of implanted substrates in short term studies. Longer sampling periods may reduce these effects of tray size, but the differential effect of colonisation sampler size on the above three indices makes it difficult to recommend future sampler design. Further experimentation is therefore necessary for the identification and recommendation of the optimal size of samplers (if any exists) as well as the optimal period for colonisation. Such methodological standardisation is highly desirable if the use of colonisation samplers, which depend on mimicking the natural assemblage, is to be extended and interstudy comparisons to be made.

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