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# Macroinvertebrate drift and community colonisation on perspex artificial substrates in the Ohinemuri River, New Zealand

I. K. G. BOOTHROYD
B. N. DICKIE
Waikato Regional Council
3 Cook Street
P. O. Box 4010
Hamilton East, New Zealand

**Abstract** Macroinvertebrate colonisation of perspex multiplate artificial substrates suspended in the Ohinemuri River, New Zealand, was investigated over a 70-day period. Community development was examined in terms of the colonisation and extinction rates of the MacArthur-Wilson equilibrium model for island faunas. Although colonisation and extinction rates were equal at 35 days, permanent stability was not attained: the extinction rate and colonisation rate continued to fluctuate as new taxa continued to colonise. This lack of permanency was attributed to changes to the surface of the plates through increases in the accumulation of fine particulate matter, and to changes in the drifting fauna that affect the pool of potential colonisers. Stream drift was an important source of colonisers, especially in the initial stages of colonisation. Although many members of the New Zealand aquatic fauna have non-seasonal life cycles, and are present as larvae at all times of year, they may occur seasonally in the drift. Therefore colonisation patterns may differ seasonally. Drift was not the only source of artificial substrate colonisers.

**Keywords** artificial substrates; biomonitoring; colonisation; drift; macroinvertebrates; streams

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## INTRODUCTION

Many investigations have now been carried out on the suitability of artificial substrates for monitoring the quality of surface waters (Beak et al. 1973; Mason et al. 1973; Chadwick & Canton 1983; Lamberti & Resh 1985; Boothroyd & Dickie 1989). A significant aspect of their use is the time required for a community to develop on the introduced surface. This will, in part, depend on the aims and restrictions of the study, but more importantly on the dynamics of colonisation of macroinvertebrates within the immediate study environment (Williams & Hynes 1977). Mason (1981), for example, suggested that in water quality studies, the colonising fauna need not be so much representative as diverse and abundant. If this is the case, then the deployment period should be that which results in the greatest number of species. On the other hand, if a desired reduction in variability between substrates is to be achieved, then sufficient time is necessary for a stable community to develop. This is particularly important if communities are to be compared spatially and temporally.

Many workers have described the colonisation of artificial and introduced substrates (Townsend & Hildrew 1976; Meier et al., 1979) and others have attempted to model the colonisation process (e.g., Minshall et al. 1983; Sheldon 1984). MacArthur & Wilson (1963), proposed an equilibrium model for island faunas to describe patterns of species diversity amongst relatively homogeneous habitat "patches". Their model predicts that the rate of colonisation or immigration will be high initially, and become progressively slower until finally an asymptote is neared. This occurs because the chances of a new species arriving decreases over time. As more species arrive, so the chances of some of them leaving, or becoming extinct, increases until the community reaches a state of dynamic equilibrium when the colonisation and extinction rates are equal, and the situation stabilises with a constant species number.

Minshall & Petersen (1985) developed the MacArthur-Wilson model further with respect to macroinvertebrate community structure in streams.

They suggested that the process leading to community equilibrium, or a stable species number, is initiated by largely stochastic events that create a non-equilibrium phase characterised by random, non-interactive conditions before leading to more deterministic equilibrium phases characterised by biotic, interactive conditions. This process then leads to better adapted community assemblages and results in a reduction in the rate of species turnover (McCormick & Cairns 1990). The hypothesis of Minshall & Petersen further predicted that during the non-equilibrium phase, the proportions of organisms colonising a patch and occurring in the stream drift should be more similar than during equilibrium. Non-equilibrium was defined by Minshall & Petersen (1985) as a phase in the colonisation process where the number of species and individuals are less than, or exceed, the equilibrium number.

Stream drift is generally regarded as the major colonisation pathway in lotic environments (Townsend & Hildrew 1976; William & Hynes 1977; Winterbourn 1982; Minshall et al. 1983; Sagar 1983). Minshall & Petersen (1985) considered drift to be a random assemblage of organisms and as such it can therefore be seen as a measure of immigration and emigration in streams.

The present study was initiated to assess the suitability of perspex multiplate artificial substrates for use in New Zealand streams and rivers. This paper presents the results of a study undertaken to determine an optimum deployment period for a stable community to develop on the artificial substrates, and to investigate the dynamics of the colonising process in terms of the MacArthur & Wilson (1963) equilibrium model.

## STUDY SITE

The work was carried out in the Ohinemuri River, which originates in the Waihi basin on the Coromandel Peninsula, North Island, New Zealand. The river has several small tributaries, and flows west to join the Waihou River which discharges into the Firth of Thames. The main land use within the Ohinemuri River catchment is pastoral farming and horticulture. The study side (37°23′S, 175°52′E), was situated west of Waihi, and the substrates were placed in a run (mean velocity range 0.24–0.56 m $s^{-1}$), c. 10 m wide and 0.6 m deep. The natural substrate consisted of small rocks, gravels, and sands, with stands of *Potamogeton crispus* L. and *Lagarosiphon major* (Ridley) Moss ex Wager also present. Further details were given by Boothroyd & Dickie (1989). The site was chosen as representative of the natural conditions expected during future monitoring programmes in the vicinity.

## METHODS

### Artificial substrates

Twenty-eight perspex multiplate artificial substrates were deployed in the Ohinemuri River from 25 August 1987 to 5 November 1987. Substrates were modified from the design of Hester & Dendy (1962), and consisted of 14 roughened perspex square plates mounted on a central bolt with eight upper spacers of 3 mm thickness and five lower spacers of 6 mm thickness. The total area available for colonisation on each substrate was 0.16 $m^2$. The substrates were bolted in pairs to warratah standards already set in the stream bed, with one substrate just above the stream bed and the second placed in the centre of the water column.

Four substrates were removed on seven occasions over the 70-day period. Recommended deployment periods for artificial substrates are generally between four and eight weeks, so substrates were removed every seven days during this period, and every 14 days thereafter. Substrates were removed in a sequential manner by moving up stream with a 250 μm mesh hand net that was placed around the substrates to prevent organisms from being swept away. In the laboratory, the substrates were dismantled and scraped clean, and all macroinvertebrates sorted and enumerated.

### Drift

Drift samples were taken during the study period using samplers similar to those described by Elliott (1970). They consisted of a metal frame with a 0.06 $m^2$ inlet and a wider outlet to which was attached a removable, one-metre long conical collecting net (250 μm mesh). Two samplers were placed in the river, 10 m up stream of the artificial substrates, on each sampling occasion. Samples were taken for a 2-hour period at dusk (c. 1800–2000 hours) every 14 days from Day 14, to Day 56 (inclusive) of the study. Samples were returned to the laboratory where all macroinvertebrates were counted and identified. Water velocity at the sampler inlet was measured at the beginning and end of each sampling period with a small Ott current meter.

### Treatment of results

Faunal colonisation and extinction rates were calculated following the method of Dickson & Cairns

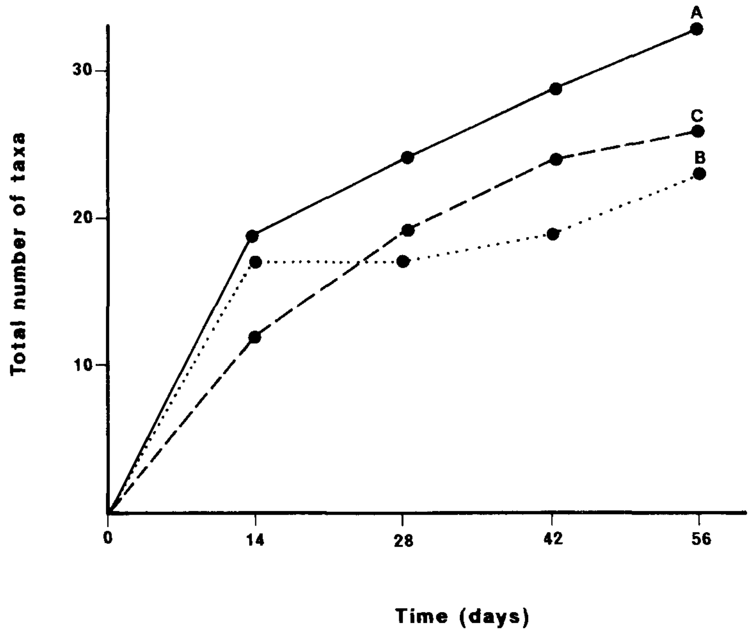

**Fig. 1** Cumulative number of taxa colonising perspex artificial substrates and occurring in drift. A, Drift and artificial substrates combined; B, Drift; C, Artificial substrates

(1972) and Stauffer et al. (1976). The total number of taxa, the number of new taxa (taxa that had not been recorded before), the number of recurring taxa (taxa eliminated that subsequently reappeared), and the number of taxa eliminated (taxa that occurred in the previous sample, but were now absent), were recorded for each sampling date. Colonisation rate was calculated as the number of new taxa plus the number of recurring taxa divided by the time (in days) between the sampling periods. Similarly, extinction rate was calculated by dividing the number of taxa eliminated by the time in days. Turnover rates were calculated as: $(CR + ER)/(S_1 + S_2)$, where $CR$ = colonisation rate, ER = extinction rate, and $S_1$ and $S_2$ are the number of taxa at the beginning and end of the sampling period, respectively (McCormick & Cairns 1990).

A $\chi^2$ analysis $(2 \times k)$ of drift and artificial substrate macroinvertebrate community abundance was carried out for each sampling occasion. The null hypothesis was that there was no association between the two classifications. Jaccards coefficient of similarity, $j = c/(a + b - c)$ where $a$ and $b$ are the number of taxa in communities A and B, and $c$ is the number of taxa common to both communities, was calculated to compare the substrate and drift faunas on each sampling date. Diversity was measured with the Shannon-Weiner Diversity Index ($H'$) (Shannon & Weaver 1949).

**Table 1** Macroinvertebrate colonisation of perspex artificial substrates in the Ohinemuri River. See text for details.

| Day | Total no. of taxa | New taxa | Recurring taxa | Eliminated taxa | Colonisation rate taxa per day | Extinction rate taxa per day | Turn-over rate |
|---|---|---|---|---|---|---|---|
| 14 | 12 | 12 | 0 | 0 | 0.86 | 0.00 | 0.072 |
| 28 | 18 | 7 | 0 | 1 | 0.50 | 0.07 | 0.019 |
| 35 | 18 | 3 | 1 | 4 | 0.57 | 0.57 | 0.032 |
| 42 | 17 | 2 | 0 | 4 | 0.29 | 0.57 | 0.025 |
| 49 | 14 | 0 | 2 | 4 | 0.29 | 0.57 | 0.028 |
| 56 | 15 | 2 | 1 | 2 | 0.43 | 0.29 | 0.025 |
| 70 | 16 | 3 | 0 | 2 | 0.21 | 0.14 | 0.011 |

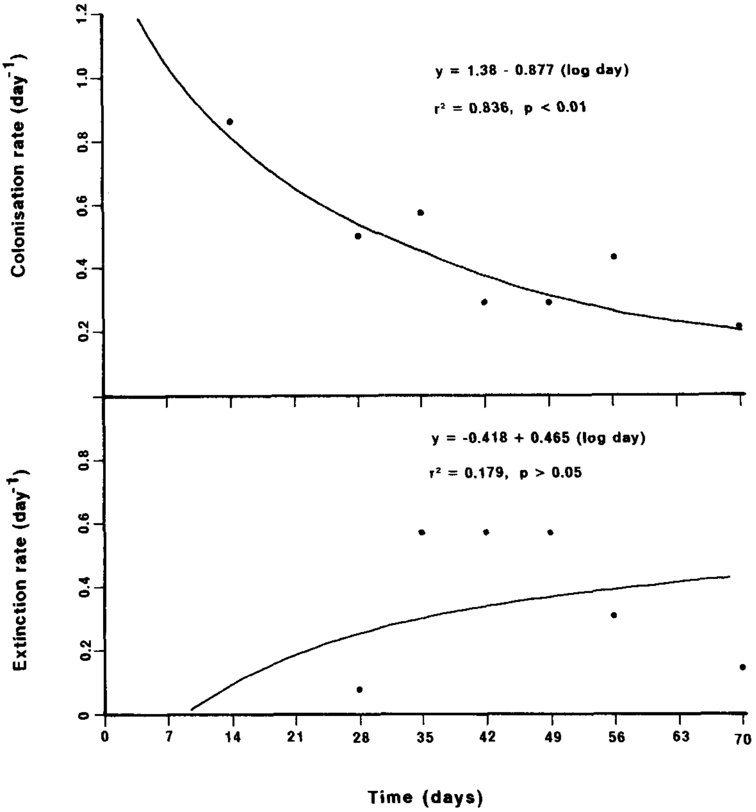

**Fig. 2** Macroinvertebrate colonisation and extinction rates on perspex artificial substrates.

## RESULTS

### Colonisation of artificial substrates

Most taxa were recorded on artificial substrates after 28 and 35 days (Table 1), although new taxa continued to colonise throughout the study period (Table 1, Fig. 1). Less than 20% of the colonisers that left the artificial substrates recolonised at a later date. The total pool of taxa available for colonisation (Fig. 1A) was always greater at any single time than the number of taxa in the drift (Fig. 1B), or already colonising the artificial substrates (Fig. 1C). The number of taxa in the drift was initially higher than the number on the artificial substrates but after Day 14 this situation was reversed.

Colonisation followed the predictions of the asymptotic model, with a high initial rate and exhibited a significant negative relationship with the logarithm of time ($P < 0.01$, Fig. 2). However, the decrease in colonisation rate was not constant, and increases occurred between Days 28 and 35, and again between Days 49 and 56. In contrast, the slope of the line describing change in the extinction rate with time was not significantly different from zero ($P < 0.05$, Fig. 2); extinction rates first increased, then stabilised before decreasing.

The MacArthur-Wilson model predicts that community structure will stabilise at an equilibrium level when the colonisation rate and extinction rate are equal. This occurred after 35 days but as both the colonisation and extinction rates continued to fluctuate, a true equilibrium level was difficult to pinpoint. Turn-over rate at the equilibrium point (Day 35) was 0.032 (Table 1).

### Drift

Ten of the taxa that occurred on artificial substrates were not taken in the drift, and nine taxa were recorded from the drift but did not colonise the substrates (Table 2). This may have been a consequence of the dusk drift sampling regime, although preliminary studies indicated that dusk drift was representative of the proportions of taxa in the full 24-hour drift in the Ohinemuri River (Boothroyd 1988). Nevertheless, some drifting taxa may not have been recorded in the drift samples.

**Table 2** Macroinvertebrate abundance (%) in pairs of drift samples (D, $n = 2$) and from artificial substrates (AS, 4 per sampling day), and co-efficients of variation (CV) for total number ($N$) and taxonomic richness ($S$).

| | Day 14 | | Day 28 | | Day 42 | | Day 56 | |
|---|---|---|---|---|---|---|---|---|
| Taxa | D | AS | D ($n = 1$) | AS | D | AS | D | AS |
| **Platyhelminthes** | 0.9 | – | – | – | – | – | 0.2 | – |
| **Annelida** | | | | | | | | |
| Naididae | 0.1 | 0.2 | 4.3 | 1.0 | 9.1 | 0.08 | 2.8 | – |
| Oligochaeta. (excl. Naididae) | 6.7 | 0.1 | 0.9 | – | 0.1 | – | – | – |
| Hirudinea | – | – | – | – | – | – | – | 0.01 |
| **Mollusca** | | | | | | | | |
| *Potamopyrgus antipodarum* (Gray) | 0.2 | – | – | 0.4 | – | 0.06 | 0.1 | 0.1 |
| **Crustacea** | | | | | | | | |
| *Paracalliope fluviatilis* (Thomson) | 0.3 | 0.3 | 0.6 | 0.6 | 0.6 | 0.8 | 1.5 | 1.0 |
| **Arachnida** | | | | | | | | |
| Acarina | – | – | – | 0.02 | – | – | – | – |
| **Ephemeroptera** | | | | | | | | |
| *Deleatidium* sp. | – | 0.03 | – | 0.04 | – | – | – | – |
| *Atalophlebioides cromwelli* (Phillips) | – | – | – | 0.02 | – | 0.24 | – | 0.3 |
| *Zephlebia* sp. | – | – | – | – | – | 0.1 | – | – |
| Leptophlebiidae | – | – | – | – | 0.5 | – | 0.2 | – |
| **Plecoptera** | | | | | | | | |
| *Acroperla trivacuata* (Tillyard) | 1.2 | 0.5 | – | 1.2 | – | 0.02 | – | – |
| *Zelandobius furcillatus* (Tillyard) | – | – | – | – | – | 0.05 | – | 0.03 |
| **Odonata** | | | | | | | | |
| *Xanthocnemis zealandica* (McLachlan) | 0.2 | – | – | – | 0.5 | 0.02 | – | – |
| **Trichoptera** | | | | | | | | |
| *Aoteapsyche colonica* (McLachlan) | 0.2 | 0.1 | – | 1.0 | – | 1.3 | 0.9 | 1.1 |
| *Aoteapsyche raruraru* (McFarlane) | – | – | – | 0.04 | – | 0.5 | 0.5 | 0.5 |
| *Oxyethira albiceps* (McLachlan) | 7.8 | 0.2 | 9.4 | 1.0 | 6.7 | 6.0 | 4.4 | 1.2 |
| *Paroxyethira hendersoni* (Mosely) | 1.7 | – | – | – | – | – | 0.1 | 0.01 |
| *Hydrobiosis parumbripennis* McFarlane | 0.3 | – | – | 0.3 | 0.1 | 0.3 | 0.2 | 0.7 |
| Hydrobiosidae indet. | 0.2 | 0.1 | – | 0.2 | – | 0.1 | – | 0.02 |
| *Psilochorema* sp. | – | – | – | 0.02 | – | – | – | – |
| *Hydrobiosella mixta* (Cowley) | – | – | – | – | – | 0.02 | – | – |
| *Pycnocentrodes* sp. | – | – | – | 0.02 | – | – | – | – |
| *Pycnocentrella eruensis* Mosely | – | 0.1 | – | 0.1 | – | – | – | 0.1 |
| **Megaloptera** | | | | | | | | |
| *Archichauliodes diversus* (Walker) | – | – | – | – | – | – | 0.1 | – |
| **Hemiptera** | | | | | | | | |
| *Sigara* sp. | – | – | – | – | – | – | 0.1 | – |
| **Coleoptera** | | | | | | | | |
| Elmidae | – | – | – | – | 0.1 | – | 0.1 | – |
| Hydraenidae | – | – | – | – | – | – | 0.1 | – |
| **Diptera** | | | | | | | | |
| *Austrosimulium australense* (Schiner) | 16.2 | 23.7 | 12.5 | 43.0 | 28.6 | 48.8 | 44.1 | 34.0 |
| *Aphrophila neozelandica* (Edwards) | 0.2 | 0.3 | – | 0.04 | 0.1 | 0.05 | 0.1 | 0.1 |
| Psychodidae | 0.2 | – | – | – | – | – | – | – |
| Chironomidae | 64.8 | 75.0 | 72.0 | 52.0 | 54.3 | 41.6 | 44.7 | 60.5 |
| *Culex pervigilans* Bergroth | 0.2 | – | 0.6 | – | – | – | – | – |
| **Taxonomic richness ($S$)** | 17 | 12 | 7 | 18 | 11 | 17 | 17 | 15 |
| **Mean number of taxa** | 13.5 | 11.8 | 7.0 | 16.0 | 8.0 | 16.8 | 14.0 | 17.0 |
| **CV (%)** | 9.4 | 35.3 | NA | 0.5 | 31.0 | 10.5 | 30.3 | 24.4 |
| **Total macroinvertebrates ($N$)** | 644 | 3758 | 352 | 5014 | 1576 | 6331 | 1820 | 9438 |
| **Mean number of macroinvertebrates** | 322.0 | 939.5 | 352.0 | 1253.5 | 788.0 | 1582.8 | 910.0 | 2359.5 |
| **CV (%)** | 58.4 | 97.8 | NA | 24.47 | 17.6 | 90.6 | 1.9 | 45.6 |

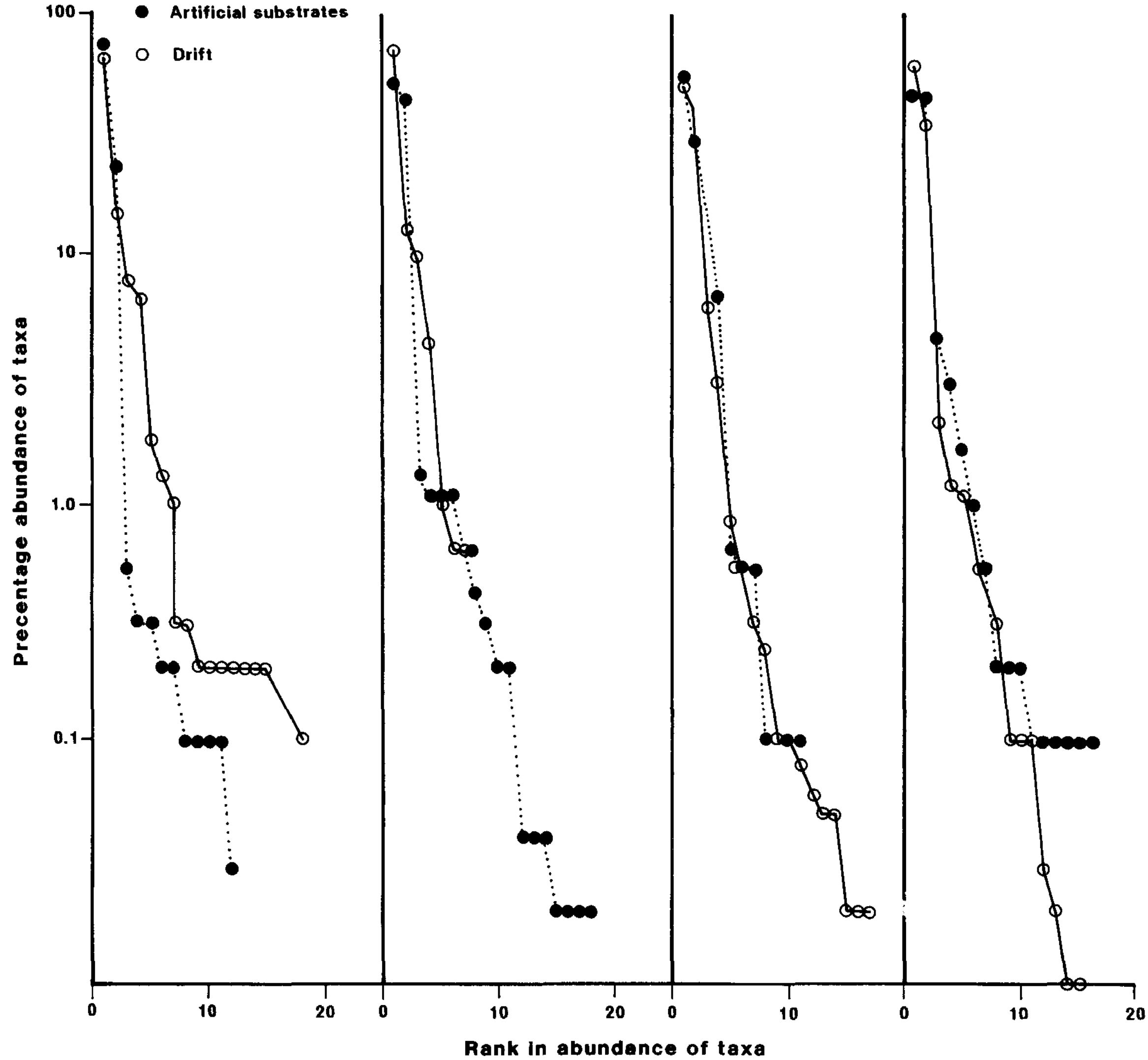

**Fig. 3** Species-abundance patterns for macroinvertebrate drift and artificial substrate colonisation in the Ohinemuri River.

*Archicauliodes diversus*, *Sigara* sp., and Coleoptera were recorded only once in the drift, and did not colonise the artificial substrates. Conversely, the cased caddis larvae *Pycnocentrodes* spp. and *Pycnocentrella eruensis* were not recorded in the drift but occurred on the artificial substrates. Chironomid larvae were the most abundant taxa in both drift and artificial substrate assemblages, except on Day 56 in the drift, and on Days 35 and 42 on the substrates, when *Austrosimulium australense* dominated.

## Drift and artificial substrate macroinvertebrate communities

The null hypothesis that there was no association between the proportions of taxa in the drift and colonising artificial substrates on each sampling date was rejected ($P < 0.001$, Table 3). Minshall & Petersen (1985) considered that species-abundance relationships between a small patch and drift should be more similar during non-equilibrium stages than equilibrium stages. No distinct differences in the patterns of fauna in the drift and colonising artificial substrates were apparent from species-abundance curves (Fig. 3). Data pooled from each sampling date exhibited significant relationships between the logarithm of percentage abundance of taxa, and rank abundance, for both drift ($r^2 = 0.832, P < 0.001$), and taxa colonising the artificial substrates ($r^2 = 0.816, P < 0.001$). Correlation co-efficients describing the relationship between mean drift rate and mean densities of common taxa colonising artificial substrates based on all sampling dates were not significant.

Similarity of taxa between drift and artificial substrate communities was greatest initially, and increased again towards the end of the study (Table 4). Except on Day 28, community diversity was always greatest in the drift, especially during the initial stages of colonisation (Table 4).

## DISCUSSION

Colonisation is a dynamic process that can be measured by the MacArthur-Wilson equilibrium model as a summation of gains and losses. If there is a finite number of individuals that the substrate (= island) can hold then the model predicts that the fauna will stabilise when the rates of gain and loss are equal. There are several advantages in using artificial substrates as islands for testing the model: artificial substrates are simple, can be precisely defined, and experiments can be replicated.

**Table 3** $\chi^2$ values and number of taxa compared ($N$) for comparison of the proportions of individual taxa in the drift and colonising artificial substrates on each sampling date. $P < 0.001$ for all sampling dates

| Day | $\chi^2$ | $N$ |
|---|---|---|
| 14 | 736.1 | 19 |
| 28 | 374.1 | 20 |
| 42 | 1004.9 | 19 |
| 56 | 531.5 | 23 |

Whereas the colonisation rate followed the asymptotic predictions of the model, and an equilibrium point was reached after 35 days, permanent stability of the macroinvertebrate community on artificial substrate was not attained. This may have resulted, in part, from the loss of the less abundant and rare taxa that did not recolonise, even though new taxa continued to settle on the perspex surfaces.

The model assumes a constant and unchanging source of colonists; in the present study, although the cumulative pool of potential colonists was always greater than the number of taxa actually colonising the artificial substrates, the pool nonetheless continued to increase. In contrast, after Day 14 the number of taxa colonising the artificial substrates was greater than the potential pool of immigrants in the drift. This overlap suggests that drift was not the only source of colonists. *Pynocentrodes* spp. and *Pynocentrella eruensis* were not recorded from the drift, but were taken from the artificial substrates; they may have used the warratah uprights as a migration route. Alternatively, oviposition by adult insects could have resulted in the presence of some taxa, including the dominant Chironomidae and Simuliidae, and egg masses and small larvae were recorded from both substrates and warratah uprights.

The presence of new taxa in the drift at different times will also alter the pool of potential colonisers, and new taxa were found colonising the substrates throughout the study period. Over 50% of the drift taxa were found on the substrates on at least one occasion. Similarity between the proportions of taxa in the drift and on the artificial substrates was highest initially when the colonisation rate and drift diversity were both greatest. Turn-over rates of colonising taxa were also greatest initially, and suggest that colonisation is largely a chance event in its early stages.

**Table 4** Similarity ($J$), and diversity ($H'$) of the artificial substrate fauna and drift fauna on each sampling date.

| Day | No. of taxa on substrates | No. of taxa in drift | Common taxa | $J$ | $H'$ substrates | $H'$ drift |
|---|---|---|---|---|---|---|
| 14 | 12 | 17 | 10 | 0.53 | 0.664 | 1.382 |
| 28 | 18 | 7 | 5 | 0.25 | 0.960 | 0.958 |
| 42 | 17 | 11 | 8 | 0.40 | 1.049 | 1.167 |
| 56 | 15 | 17 | 10 | 0.45 | 0.829 | 10.59 |
| Total | 24 | 23 | 15 | 47 | – | – |

As the artificial substrates were initially devoid of any biota or periphyton, continuing changes in habitat may have been responsible for changes in macroinvertebrate communities. Dickson & Cairns (1972), and Stauffer et al. (1976), in similar colonisation studies using artificial webbing as substrates, concluded that permanent stability in the number of colonising taxa did not occur owing to a lack of diverse habitat, and presumably a failure to reach a truly mature and interactive community of organisms. Similarly, Meier et al. (1979) suggested that continued colonisation by new taxa, and increasing community diversity over the 60-day study period and a consequent lack of equilibrium, resulted from the creation of new microhabitats. This occurred largely through the accumulation of periphyton and detritus, and the emergence of adult insects.

Both mechanisms are likely to be true for the perspex artificial substrates. Boothroyd & Dickie (1989) showed that colonisation by some taxa was correlated with a build-up of fine particulate organic matter (FPOM), whereas other taxa such as *A. australense* larvae were inhibited by a lack of clean substrate for attachment. In his study of an artificially shaded Waitakere River, Towns (1983) also found that the presence or absence of periphyton influenced the distribution of several species through interference with both attachment sites and feeding habits. Departure and extinction rates in other colonisation studies have also been attributed to a lack of FPOM (Townsend & Hildrew 1976; Lake & Doeg 1985; Benson & Pearson 1987). Changes in the habitat conditions on the substrate surface will therefore affect the suitability for colonisation by different organisms. If the substrate is no longer suitable for a taxon (e.g., no organic layer, insufficient refuge, or no prey species), then this taxon will be excluded from the pool of potential colonisers.

Significant associations between the proportional abundance of taxa in the drift and colonising the artificial substrates also suggest that an equilibrium stage was not reached, and that the colonising process continued in the absence of hypothesised biotic interactions (competition, predator-prey relationships) (Minshall & Petersen 1985). This may have been a consequence of the small number of sampling occasions (4), or the length of the study period. On the other hand, the dynamics of macroinvertebrate colonisation in New Zealand streams may not reach an equilibrium level, as defined by the model. Many members of the New Zealand aquatic fauna exhibit non-seasonal and poorly synchronised life cycles (Towns 1981; Winterbourn et al. 1981; Boothroyd 1987), and individuals are present in all life stages at all times of the year. Whereas seasonal influences may thus be less apparent, a continuous immigration of individuals in all life stages may influence biotic interactions to such an extent that mature equilibrium community assemblages cannot be reached. At the same time such life cycles may have evolved to avoid such interactions. Scrimgeour et al. (1988) and Boothroyd & Dickie (1989) found no evidence to suggest any succession of taxa in macroinvertebrate communities colonising natural and artificial substrates, respectively.

Whereas many members of the New Zealand aquatic fauna may exhibit non-seasonal life cycles, this may not apply equally to the occurrence of taxa in the drift. For example, larvae of some chironomid species show little propensity to drift in winter and early spring, even though they may be abundant in the benthos (Boothroyd pers. obs). Likewise, McLay (1968) found that lowest drift rates were recorded during winter, when many taxa were not taken in drift samples. This is in accordance with the general observation that drift rates are not related in a density-dependent manner to benthic invertebrate abundance (Minshall & Petersen 1985). In studies on Australian rivers, Benson & Pearson (1987) found that colonisation differed in the wet and dry seasons, colonisation being faster in the wet season when drift densities were also greatest.

In conclusion, a period of 35 days appeared to enable an equilibrium community to develop on perspex artificial substrates in the Ohinemuri River; but the community did not stabilise, and colonisation and extinction rates continued to vary. In terms of the MacArthur-Wilson model, this lack of permanency in the species number that colonised the artificial substrates can therefore be seen as a stochastic community development process, shaped by prevailing abiotic and environmental factors as opposed to biotic interactions. In addition, life history characteristics of the fauna appears to play a significant, but as yet undetermined, role in the colonising process. Drift was an important source of macroinvertebrates colonising the perspex substrates, but was by no means the only colonising pathway.

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