

## **Vertical Distribution of Benthic Invertebrates in the Bed of the Thomson River, Victoria**

*R. Marchant*

Museum of Victoria, 71 Victoria Crescent, Abbotsford, Vic. 3067.

### *Abstract*

The vertical distribution of the benthic fauna was studied at three sites on the Thomson River using a freeze-corer. Samples were taken over two years in early and late summer. At each site an average of 72 to 84% of the fauna was found in the 0-10 cm zone of the riverbed, 10-20% in the 10-20 cm zone and 6-8% in the 20-30 cm zone; flooding at one site was followed by an increase in the depth to which the fauna penetrated. Surface percentage abundances were probably underestimated because of the inability of the corer to sample surface rocks and their fauna consistently and because the coring operation disturbs the surface fauna to some extent before it can be frozen. Nevertheless, the results indicate that in the Thomson River the majority of the fauna is within the depth range (0-10 cm) of a Surber sampler.

### **Introduction**

Conventional sampling devices (e.g. Surber samplers) for obtaining quantitative samples of benthic invertebrates from rivers enable the operator to penetrate the river-bed to a depth of only 5-10 cm. Williams and Hynes (1974) demonstrated, however, that benthic fauna from the sediment surface can occur to a depth of 70 cm in gravel river-beds, thus throwing doubt on the accuracy of estimates of benthic density obtained with conventional samplers. To obtain comprehensive data on a benthic fauna, its vertical distribution within a river-bed must be known.

Studies on vertical distribution of lotic benthic invertebrates have been carried out in North America (Hynes 1974; Williams and Hynes 1974; Gilpin and Brusven 1976; Godbout and Hynes 1982; Pugsley and Hynes 1983), Europe and the U.K. (Schwoerbel 1961; Hynes *et al.* 1976; Morris and Brooker 1979; Bretschko and Klemens 1986) and Malaysia (Bishop 1973), but not in Australia. These studies indicate that the percentage of the benthic fauna that is within 5-10 cm of the surface of the substratum, i.e. within the range of conventional samplers, is variable. This undoubtedly reflects not only actual differences between sites, but also the influence of errors in methods for assessing vertical distribution.

This paper examines the vertical distribution of the benthos (assessed using a freeze-corer) at a number of sites on the Thomson River, Victoria. It also compares estimates of surface (i.e. 0-10 cm) benthic densities derived from these data with those obtained at the same time with a Surber sampler; such a comparison has not been made by previous users of freeze-corers. The primary aim is, however, to provide data on the vertical distribution of a benthic fauna which has not been sampled before for this feature.

## Study Area and Methods

The study area on the Thomson River (approximately 37°50'S., 146°25'E.), which is within 35 km of the Thomson Dam, has been fully described by Davey *et al.* (1987). Three sites were selected (T6, T16, T21A) at which benthic samples had previously been taken (Doeg *et al.* 1987): T6 is 35 km upstream of the dam wall while T16 is 10 km and T21A 33 km downstream. The substratum was composed of cobbles, pebbles and gravel at each site; mean grain size varied from 16 to 24 mm for sediment fractions >2 mm in size; width varied from 7 to 30 m and water depth from 10 to 40 cm. All sites were surrounded by mixed-species *Eucalyptus* forest.

To quantify the vertical distribution of the benthic invertebrates at each site, cores were taken with a freeze-corer on four occasions: in March and December in both 1985 and 1986. A detailed description of the freeze-corer and its use is given by Marchant and Lillywhite (1988). The corer consists of a heavy standpipe with a conical steel driving tip; the whole assembly is hammered 30 cm into the river-bed and left for 24 h before freezing. Liquid CO<sub>2</sub> is then discharged from nozzles on a probe into the lower end of the standpipe, producing dry ice and freezing the surrounding water and sediment to the pipe. Three cores were taken at each site on each sampling occasion, although up to five cores were taken occasionally at T16. The c. 30 cm long cores that resulted were cut into 10-cm sections and placed in pre-weighed plastic bags for transport to the laboratory. Three depth zones in the river-bed were thus sampled: 0–10 cm, 10–20 cm and 20–30 cm.

In the laboratory, the wet weight of each section of a core was measured to the nearest gram. Each section was then placed on a 150- $\mu$ m sieve and any mud and silt was washed through into a container and later dried and weighed. Benthic invertebrates and associated organic matter were separated from the residual inorganic sediments by flotation in a strong solution of calcium chloride and stored in 70% ethanol; the residue was searched for cased invertebrates. Subsequently, the fauna was sorted and identified under low magnification. The inorganic sediments were fractionated using a series of Wentworth sieves and weighed (for details see Marchant and Lillywhite 1988). The volume of the sediment in each section of core was measured by displacing water from a large container; the volume of water in the core was estimated as the difference between the wet weight of each section and the dry weight of the inorganic sediments (including mud and silt). Total volume and mean cross-sectional area could thus be calculated, given that the length of each section was 10 cm.

Ten samples of the benthic fauna were taken with a Surber sampler (area 500 cm<sup>2</sup>; 150- $\mu$ m mesh net) at each site on each sampling occasion. The sampling area of the Surber sampler was enclosed on three sides and on the top with 150- $\mu$ m mesh; a hole for the operator's arm remained in the top. Thus, there was little possibility of invertebrates from outside the sampling area contaminating a sample. Material was removed by hand to a depth of about 10 cm. The lighter organic component of each sample was separated by elutriation in the field and preserved in 2% formaldehyde. In the laboratory, invertebrates were separated from residual sediment with calcium chloride, as before, and stored in 70% ethanol. A 10% subsample of each sample was taken with a subsampler described by Marchant (1988). The fauna was sorted from each subsample and identified under low magnification. Surber estimates of benthic density were converted to logarithms before calculating 95% confidence limits (95% C.L.), as outlined by Elliott (1977).

## Results

Little variation in the vertical distribution of the benthic fauna within the first 30 cm of the river-bed occurred between the sites (Table 1): approximately 70 to 90% of the individuals at each site were found in the 0–10 cm layer of the cores, 6–20% in the 10–20 cm layer and 3–10% in the 20–30 cm layer. (The same pattern prevails even if the raw counts uncorrected for variation in sampling area are considered.) The one exception to the pattern occurred in December 1985 at T6 when a substantial proportion of the fauna (60%) was found at depths greater than 10 cm; this occurred during a period of higher than normal flow (approximately 2–3 times base flow). The increase in the density of the fauna at depths exceeding 10 cm on this occasion suggests that the benthos responded to flooding by penetrating more deeply into the river-bed. Presumably, some of the fauna in the 0–10 cm layer was also washed away by the flood, further lowering the values for percentage abundance in this depth zone. A similar response was not seen at T16 on this occasion, as this site was downstream of the dam and flow did not exceed normal base flow in this region.

The total numbers of taxa in the cores decreased as depth increased, with maximum numbers at 0–10 cm. The total numbers in this zone were lower than the total numbers found in the Surber samples, reflecting the fact that the Surber values were based on more samples (30–40 versus 9–17 samples). A few rare taxa were taken only in the cores but not in the Surber samples.

Mean densities in the 0–10 cm layer of each core were always lower than those recorded from the Surber samples (Table 1). In no case did the 95% confidence limits of the Surber estimates of density overlap the mean densities in the 0–10 cm zone of the cores. Confidence limits for density estimates from the cores were not calculated because too few cores were taken to justify this.

**Table 1. Mean density of individuals ( $10^{-3} \times \text{numbers m}^{-2}$ ) and total number of taxa ( $S$ ) at various depths from frozen core samples and from Surber samples from the Thomson River**

The percentage each value represents of the total for each core is given in brackets as are the 95% C.L.s of the Surber samples;  $n$ , number of cores

|                   | Core samples |          |          | $n$ | Surber samples   |
|-------------------|--------------|----------|----------|-----|------------------|
|                   | 0–10 cm      | 10–20 cm | 20–30 cm |     |                  |
| T6                |              |          |          |     |                  |
| $S^A$             | 61           | 35       | 15       |     | 158              |
| Mar 85            | 19.9 (86)    | 2.5 (11) | 0.8 (3)  | 3   | 35.1 (26.4–46.6) |
| Dec 85            | 7.1 (40)     | 8.5 (47) | 2.2 (13) | 3   | 14.6 (10.3–20.6) |
| Mar 86            | 13.4 (67)    | 4.6 (23) | 1.9 (10) | 3   | 43.4 (34.5–54.6) |
| Dec 86            | 7.8 (74)     | 1.8 (17) | 0.9 (9)  | 3   | 28.1 (20.9–37.8) |
| Mean <sup>A</sup> | 13.7 (77)    | 3.0 (17) | 1.2 (6)  |     | 35.5             |
| T16               |              |          |          |     |                  |
| $S$               | 46           | 22       | 8        |     | 129              |
| Mar 85            | 7.4 (84)     | 1.1 (13) | 0.2 (3)  | 3   | 13.1 (11.2–15.3) |
| Dec 85            | 9.1 (89)     | 0.6 (6)  | 0.5 (5)  | 5   | 22.5 (18.1–28.0) |
| Mar 86            | 4.4 (79)     | 0.7 (12) | 0.5 (9)  | 4   | 13.8 (11.2–17.0) |
| Dec 86            | 2.3 (79)     | 0.4 (13) | 0.2 (8)  | 5   | 19.8 (17.3–22.6) |
| Mean              | 5.8 (84)     | 0.7 (10) | 0.4 (6)  |     | 17.3             |
| T21A <sup>B</sup> |              |          |          |     |                  |
| $S$               | 33           | 25       | 8        |     | 86               |
| Mar 85            | 4.5 (73)     | 1.3 (20) | 0.4 (7)  | 3   | 17.0 (12.0–24.0) |
| Mar 86            | 9.3 (68)     | 3.1 (23) | 1.3 (9)  | 3   | 30.2 (24.5–37.3) |
| Dec 86            | 6.5 (80)     | 1.2 (14) | 0.5 (6)  | 3   | 29.5 (20.2–43.1) |
| Mean              | 6.8 (72)     | 1.9 (20) | 0.7 (8)  |     | 25.6             |

<sup>A</sup> Excludes data for Dec. 1985 when river was in flood.

<sup>B</sup> No samples for Dec. 1985 because river was in flood.

The average cross-sectional area of a core (40–60 cm<sup>2</sup>) was an order of magnitude smaller than the area (500 cm<sup>2</sup>) sampled by each Surber sample. This was reflected in higher coefficients of variation (CV) for surface densities in the core samples (7 out of 11 greater than 50%) than in the Surber samples (20–50%). Nevertheless, sampling errors associated with the core samples were not so great that they obscured the consistent decrease with depth of the density and percentage abundance of the fauna at each site.

The percentage abundances of the major taxa (>1% of total numbers at a site) at various depths are given in Table 2. In interpreting these data it must be remembered that a mean density of 200 m<sup>-2</sup> per 30 cm core implies that one specimen was present on average per core of 40–60 cm<sup>2</sup> cross-sectional area.

**Table 2. Percentage abundances of major taxa at various depths at each site on the Thomson River, pooled over all sampling occasions**

The total number of individuals ( $N$ ) extracted from all cores and the mean abundance per 30-cm core (numbers  $m^{-2}$ ) are also shown. Percentage abundances, mean abundances and  $N$  during December 1985 at T6, when the river was in flood, are given in parentheses

| Taxon                      | Depth (cm) |         |         | $N$       | Mean abundance |
|----------------------------|------------|---------|---------|-----------|----------------|
|                            | 0-10       | 10-20   | 20-30   |           |                |
| T6                         |            |         |         |           |                |
| Oligochaeta                | 68         | 32      | —       | 8         | 155            |
| Gordiidae                  | —          | 50 (63) | 50 (37) | 7 (8)     | 134 (512)      |
| Hydracarina                | 83 (23)    | 17 (69) | — (8)   | 20 (21)   | 404 (1232)     |
| Leptophlebiidae            | 93 (76)    | 5 (24)  | 2       | 191 (24)  | 3949 (1569)    |
| Plecoptera                 | 85 (78)    | 15 (14) | — (8)   | 16 (17)   | 324 (1170)     |
| <i>Agapetus</i> sp.        | 82 (80)    | 9 (20)  | 9       | 60 (4)    | 1240 (264)     |
| Other Trichoptera          | 45 (71)    | 33 (20) | 22 (9)  | 110 (16)  | 2154 (1083)    |
| Elmidae                    | 82 (44)    | 14 (50) | 4 (6)   | 119 (26)  | 2420 (1601)    |
| Other Coleoptera           | 80 (62)    | 17 (38) | 3       | 38 (8)    | 766 (565)      |
| Chironomidae               | 77 (30)    | 17 (55) | 6 (15)  | 246 (123) | 4979 (7638)    |
| Other Diptera              | 61 (14)    | 30 (63) | 9 (23)  | 65 (33)   | 1274 (2042)    |
| T16                        |            |         |         |           |                |
| Oligochaeta                | 96         | 4       | —       | 86        | 1005           |
| Gordiidae                  | 46         | 28      | 26      | 30        | 386            |
| Hydracarina                | 100        | —       | —       | 13        | 153            |
| <i>Jappa</i> sp.           | 56         | 30      | 14      | 14        | 169            |
| Other Leptophlebiidae      | 92         | 8       | —       | 42        | 487            |
| Plecoptera                 | 95         | 5       | —       | 18        | 210            |
| Philorheithridae           | 94         | 4       | 2       | 133       | 1567           |
| Other Trichoptera          | 97         | 3       | —       | 26        | 304            |
| Elmidae                    | 79         | 13      | 8       | 56        | 669            |
| Chironomidae               | 76         | 12      | 12      | 123       | 1508           |
| Other Diptera              | 73         | 27      | —       | 20        | 225            |
| Odonata                    | 54         | 46      | —       | 6         | 65             |
| T21A                       |            |         |         |           |                |
| Oligochaeta                | 100        | —       | —       | 10        | 374            |
| Gordiidae                  | 14         | 43      | 43      | 15        | 514            |
| Gastropoda                 | 80         | 14      | 6       | 43        | 1541           |
| Hydracarina                | 76         | 24      | —       | 20        | 688            |
| Oribatidae                 | 86         | 14      | —       | 11        | 391            |
| <i>Tasmanocoenis</i> spp.  | 73         | 21      | 6       | 41        | 1437           |
| <i>Coloburiscoides</i> sp. | 75         | 17      | 8       | 14        | 501            |
| Plecoptera                 | 77         | 23      | —       | 7         | 242            |
| Hydropsychidae             | 64         | 20      | 16      | 23        | 819            |
| Other Trichoptera          | 67         | 33      | —       | 5         | 167            |
| Coleoptera                 | 58         | 42      | —       | 4         | 130            |
| Chironomidae               | 75         | 19      | 6       | 61        | 2151           |
| Other Diptera              | 67         | 33      | —       | 5         | 167            |
| Odonata                    | 87         | 13      | —       | 6         | 215            |

Oligochaeta were only caught in substantial numbers at T16 where they were largely confined to the surface layer. The same distribution was found at T21A but at T6 they appeared to penetrate to 10–20 cm; the percentages at T6 are not based, however, on many specimens. In contrast, the Gordiidae were well distributed throughout the core at all sites and were generally most abundant below 10 cm.

Mollusca were abundant at T21A where *Beddomeia* sp. and *Ferrissia* sp. were found mostly in the surface layer; the former penetrated to 20–30 cm while the latter only reached 10–20 cm. At T16, a few specimens of *Pisidium casertanum* (Poli) were taken, but only at 0–10 cm. Hydracarina (and Oribatidae at T21A) penetrated to 10–20 cm at T6 and T21A, but were only found at the surface at T16.

The Ephemeroptera displayed a variety of distributions. More than 90% of the Leptophlebiidae occurred at 0–10 cm, except for *Jappa* sp. which was found down to 20–30 cm (at T16) and of which 44% occurred below 10 cm. *Tasmanocoenis* spp. (2 species) and *Coloburiscoides* sp. also penetrated to 20–30 cm, but not in the same proportions as *Jappa* sp., with more than 70% of their populations above 10 cm. The other Ephemeroptera at T6 and T16 consisted of a few specimens of *Baetis* sp. and *Tasmanocoenis* sp., which were confined to 0–10 cm.

The Plecoptera did not penetrate beyond 10–20 cm at any site and generally 80% or more were found at 0–10 cm. They consisted mostly of *Dinotoperla* spp. at T16 and T21A. At T6, species of Austroperlidae, *Stenoperla*, *Dinotoperla* and *Riekoperla* occurred.

The Trichoptera also displayed various patterns of distribution. *Agapetus* sp. was most abundant (>80% of the population) at 0–10 cm, whereas other Trichoptera at T6 were much more dispersed throughout the 30 cm of a core. This dispersion was the result of large numbers of early instar *Tamasia* sp. occurring (in one core) at all depths. If these are excluded, then the other Trichoptera at this site (consisting of larger instar *Tamasia*, *Notalina* spp., *Hydrobiosella* sp., Philorheithridae, *Asmicridea* sp., *Taschorema* sp.) were mostly concentrated at the surface (70% of the specimens) as were these taxa at T16 (>90% at the surface). At T21A, two species of *Cheumatopsyche* (Hydropsychidae), reached depths of 20–30 cm, but *Asmicridea* sp. was confined to the surface. The other Trichoptera at this site [a few *Agapetus* sp. and *Oxyethira columba* (Neboiss)] were not found below 10–20 cm.

The Elmidae (mostly two species of *Austrolimnius*) were found throughout the 30 cm cores, but were most abundant on the surface, as were the other Coleoptera at T6 which consisted of one species of Ptilodactylidae, one species of Helodidae and *Sclerocyphon maculatus* Blackburn. Other Coleoptera at T16 and T21A consisted of single specimens of *Berosus* sp. confined to 0–10 cm.

The Chironomidae and other Diptera (Tipulidae, Ceratopogonidae, Empididae, Athericidae and Tabanidae) displayed a very consistent pattern of vertical distribution. At all sites 75–77% of the Chironomidae occurred at 0–10 cm, but at each site some reached 20–30 cm. The Chironomidae were dominated at each site and at all depths by Orthocladinae and Chironomini; Aphroteniinae, Tanypodinae and Tanytarsini were present in lower numbers and at T6 Podonominae also occurred. The other Diptera were somewhat more deeply distributed with only 60–70% at the surface.

The Odonata (except at T21A), Megaloptera (*Archichauliodes* sp.), Neuroptera (*Austro-neurorthus* sp.) and Amphipoda [*Pseudomoera fontana* (Sayce)] occurred rarely and no reliance can be placed on their patterns of distribution. The Odonata at T21A (mostly *Hemigomphus* sp.) were found down to 10–20 cm, although the majority occurred at the surface.

The influence of flooding on vertical distribution was clearly seen at T6 (Table 2), where the percentage abundance of most groups decreased above 10 cm and increased below this depth in December 1985. This was particularly obvious in the Hydracarina, Elmidae, Chironomidae and other Diptera, all groups which are morphologically suited for burrowing. The Trichoptera appeared to display the opposite reaction, increasing percentage abundance at 0–10 cm; but, as indicated above, the large numbers of early instar *Tamasia* bias the normal pattern of vertical distribution at T6 which is, in fact, very similar to that which occurred during the flood.

Spearman's rank correlation coefficients ( $r_s$ ) were calculated between the 15 most common taxa in the Surber samples at each site and those in the 0–10 cm layers of the cores. Only

site T6 showed a significant correlation ( $r_s = 0.64$ ;  $P < 0.05$ ) that indicated there were no major changes in the rankings of the common taxa between the two types of sample; at the other two sites  $r_s$  values were  $< 0.4$  and non-significant. Thus, the frozen cores do not always have the same proportional representation of the common taxa as that found in the Surber samples.

**Table 3. Ratios of densities of various taxa recorded in Surber samples to those recorded in the 0–10 cm layer of frozen cores taken from sites on the Thomson River**

Samples taken at T6 in December 1985 were excluded. Dashes indicate taxon was not found or fewer than two or three individuals occurred in the 0–10 cm zone

| Taxon                                  | T6   | T16 | T21A |
|--|------|-----|------|
| Oligochaeta                            | 24.3 | 4.8 | 10.3 |
| Gordiidae                              | —    | 0.3 | 0    |
| Gastropoda                             | —    | —   | 0.7  |
| Hydracarina plus Oribatidae            | 1.6  | 0.5 | 1.7  |
| <i>Tasmanocoenis</i> spp.              | —    | —   | 6.0  |
| <i>Coloburiscoides</i> sp.             | —    | —   | 2.4  |
| <i>Jappa</i> sp.                       | —    | 3.0 | —    |
| Leptophlebiidae (except <i>Jappa</i> ) | 2.1  | 8.3 | —    |
| Plecoptera                             | 2.4  | 2.2 | 12.5 |
| <i>Agapetus</i> sp.                    | 1.3  | —   | —    |
| Philorheithridae                       | —    | 0.5 | —    |
| Hydropsychidae                         | —    | 1.6 | 6.3  |
| Other Trichoptera                      | 3.9  | 5.5 | —    |
| Elmidae                                | 2.6  | 1.1 | —    |
| Other Coleoptera                       | 2.9  | —   | —    |
| Chironomidae                           | 2.3  | 4.1 | 2.9  |
| Other Diptera                          | 1.8  | 2.2 | —    |

The ratio of the density of a taxon in the Surber samples to its density in the 0–10 cm layer of the cores nearly always exceeded one (Table 3). Only a few taxa had ratios near one: Gastropoda, Hydracarina and *Agapetus* sp. These taxa are probably less mobile than the others. In contrast, only one individual of *Baetis* sp. was caught in the cores (at T6; not shown in Table 3), whereas it was common in the Surber samples at T6 and T16. This genus is generally regarded as a strong swimmer, which suggests that the ratios in Table 3 do reflect relative mobility to some extent. The high ratios for the Oligochaeta are puzzling since they are not usually regarded as highly mobile. However, it is possible that they were more likely to be crushed than other taxa by the coring operation and thus were overlooked or not recognised in the samples. The Gordiidae had a ratio less than one; this is perhaps not surprising since they occurred mainly below 10 cm at each site (Table 2), suggesting that those that did occur in the 0–10 cm zone were at the limit of the depth range of the Surber sampler.

## Discussion

### *Problems with Freeze-coring*

It is clear that the frozen cores underestimated benthic densities in the 0–10 cm layer compared with those derived from the Surber samples. There are a number of reasons for this. First, loose rocks on the surface of the river-bed were not always retrieved in the frozen cores. This was less of a problem at T6 than at downstream sites, because water temperatures were lower at this site during coring (11–13°C) than were those downstream

(15–18°C), enabling more effective freezing especially at the surface; cores from T6 were heavier and had a wider diameter (mean values 4.1 kg, 10 cm) than those from T16 (3.2 kg, 9 cm) (Marchant and Lillywhite 1988). The loose surface rocks undoubtedly had attached fauna which was therefore not retrieved; this would result in an underestimate of density compared with that from a Surber sample. This discrepancy was least at T6 where mean core density at 0–10 cm was 39% of mean Surber density (Table 1); at T16 and T21A mean surface densities were 34% and 27%, respectively, of Surber densities.

The second reason for the discrepancy in densities between the core and Surber samples was the fact that the more mobile taxa, as outlined in Table 3, were less abundant in the core samples. This was almost certainly due to the general disturbance of the river-bed surface during the freezing operation which caused such taxa to flee before they could be frozen to the core. The vibrations resulting from walking or placing equipment near the sampling point and the change in current when the cylinder used to deflect stream flow was placed around the standpipe (see Marchant and Lillywhite 1988) would both have caused such disturbance. Bretschko and Klemens (1986) demonstrated that mobile benthic taxa could flee from these sorts of disturbances within 15 seconds of an impact. The initial hammering of the standpipe into the river-bed would also have caused disturbance. The 24-h delay between insertion and freezing gave only some time for the fauna to recover; Pugsley and Hynes (1983) delayed freezing for at least 48 h.

There is no evidence that the fauna flees horizontally from the freezing front as it progresses through the sediments. Pugsley and Hynes (1983) demonstrated this experimentally (in the laboratory) by freezing cages of natural stream substratum from one end: densities of invertebrates did not vary with distance from the freezing point, indicating that there was no horizontal migration away from the freezing front. Unfortunately, they gave no details of the composition of the invertebrate fauna in their cages of substratum. However, the site from which they extracted the substratum contained species from the same major groups of lotic invertebrates (Godbout and Hynes 1982) as were found in the Thomson River.

Disturbances of the river-bed surface probably affected fauna in the 0–10 cm zone more than that in deeper layers, where there would be less opportunity to flee by drift. Thus the percentage of the community that occurred in the uppermost layer could be higher than indicated in Table 1. Pugsley and Hynes (1983) found that 66–79% of the fauna in two stony rivers in Southern Ontario occurred in the 0–10 cm layer of their frozen cores. These percentages are much the same as those from the Thomson River. The porosities at one of their sites (21–29% for the 0–30 cm sediment layers in the Speed River, Stocker and Williams 1972) were somewhat higher than those at the three sites in the Thomson River (15–20% for the same sediment layers, Marchant 1987). Previous work at the Speed River site (Williams and Hynes 1974) had not indicated any obvious correlation between faunal abundance at a particular depth and porosity; significant positive correlations, however, occurred between oxygen concentrations or levels of organic matter at various depths and total numbers of animals. In the Thomson River, T16 showed a significant decrease in the level of coarse organic matter (particles > 150 µm) with depth, but there was no such change with depth at T6 or T21A (Marchant 1987). Obviously anoxic sediments were never retrieved at any site.

Pugsley and Hynes (1983) summarized much of the published literature on vertical distribution of stream benthos in stony streams. They concluded that mechanical corers (the Williams corer used by Williams and Hynes 1974) and colonization pots or baskets were subject to various problems which resulted in inaccurate estimates of the percentage abundance of the benthos at various depths. The Williams corer needed to be repeatedly driven and extracted to give a depth profile at a particular spot; this apparently resulted in some of the animals becoming entrained with the corer thus artificially increasing their numbers at depth. The colonization baskets were generally regarded as inaccurate because most tended to provide 'open corridors' that facilitated faunal colonization of the deeper layers of the river-bed. Pugsley and Hynes concluded that frozen cores produced the most

accurate estimates of benthic densities and percentage abundances at various depths; however, they did not compare their estimates of surface density with conventional surface samples taken at the same time.

Bretschko (1985) and Bretschko and Klemens (1986) also used frozen cores (to sample an Austrian Stream) but disagreed with Pugsley and Hynes (1983) on the accuracy of the technique. They found that, if the benthic fauna was stunned with an alternating electrical current (650 V, 50 Hz) before a core was frozen, maximum densities occurred at depths of 20–40 cm; without stunning, maximum densities were found at 0–20 cm. They suggested that this difference arose because the fauna was repelled by the freezing front, but in a vertical rather than horizontal direction, and that without pre-stunning the fauna migrated to the top of the core, presumably because the core was frozen from the bottom upwards. However, Bretschko and Klemens admitted that, when the benthos was stunned before freezing, paralysed animals in the surface layers could have drifted away in the stronger currents encountered at these depths. This would explain the lower percentage abundances in the 0–20 cm zone of these cores.

The suggestion that the benthic fauna migrates vertically during the freezing process is unlikely to apply to the cores taken in the Thomson River because freezing takes place at all depths in these cores simultaneously rather than from the bottom upward: the liquid CO<sub>2</sub> is discharged from six nozzles evenly spaced along the bottom 30 cm of the probe that is inserted into the standpipe (see Marchant and Lillywhite 1988). Bretschko and Klemens (1986) and Pugsley and Hynes (1983), on the other hand, used liquid nitrogen as a freezing agent, which was discharged at the bottom of the standpipe first and then at progressively higher levels to ensure coverage over the full length of the core. In addition, if vertical migration occurred in the Thomson River during freezing of a core, it is difficult to explain the increased percentage abundances recorded below 10 cm at T6 in December 1985 when flooding occurred.

Bretschko (1985) also recorded increased densities of certain invertebrate taxa in cores which were subject to pre-stunning. This suggests that, even at depths greater than 20 cm, some of the fauna were able to move away from surface disturbances (assuming that Pugsley and Hynes' experimental demonstration that fauna do not flee horizontally from freezing fronts is applicable to all taxa). Thus the previous conclusion that the percentage abundances in the 0–10 cm layers of cores from the Thomson River are underestimates may not be correct for all taxa. At present, it seems reasonable to conclude that the general pattern of percentage abundances given in Tables 1 and 2 is reliable even if absolute densities have been underestimated. Thus the majority of the benthic fauna in the Thomson River occurs within the depth range (0–10 cm) of a Surber sampler.

#### *Vertical Distribution of the Fauna*

Williams (1984) divided the interstitial benthos of river-beds into the permanent and occasional hyporheos (hyporheos being the term for the fauna inhabiting the interstices between the cobbles, pebbles and gravel of rocky riverbeds, known as the hyporheic zone). According to Williams (1984), the larvae and nymphs of most aquatic insects are classified as occasional hyporheos since they spend part of their life cycle out of water and must leave the hyporheic zone before they emerge as adults. As aquatic insects constitute most of the fauna in the Thomson River (Marchant 1987) it would be reasonable to characterize the fauna as dominated by occasional hyporheos. However, the Oligochaeta, Mollusca, and water mites (Hydracarina and Oribatidae) are all considered as permanent hyporheos by Williams (1984). In the Thomson River, the Gordiidae would also be considered as permanent hyporheos and are the only members of this group whose greatest percentage abundance occurs below 10 cm.

The effect of flooding in the Thomson River on the pattern of vertical distribution was to cause the fauna to move more deeply into the hyporheic zone than usual. This response

was also seen in the Speed River by Williams and Hynes (1974) when they sampled 24 h after a large spate. It was not evident 48 h after another spate nor 72 h after a spate in the River Wye in Wales (Morris and Brooker 1979); this suggests that the fauna can move back to the surface layer quickly once a flood has subsided.

The patterns of vertical distribution of individual taxa enable some conclusions to be drawn about their habits. A higher percentage of *Jappa* sp. penetrated the river-bed below 10 cm than other ephemeropteran genera; *Tasmanocoenis* spp. and *Coloburiscoides* sp. penetrated as deeply but in smaller proportions. *Jappa* has been described before as a burrowing species (Riek 1970; Williams 1980) but no quantitative indication was given of this ability. The burrowing abilities of *Tasmanocoenis* and *Coloburiscoides* were much the same, judging by their values for percentage abundance at various depths; only *Tasmanocoenis* has previously been considered as a burrower (Riek 1970). Despite this ability to penetrate the riverbed, more than 70% of the *Tasmanocoenis* population was found in the 0–10 cm zone. The Leptophlebiidae (which apart from *Jappa* consisted largely of a species of *Atalophlebioides*) were restricted (>90% of the population) to the surface layer as Williams and Hynes (1974) recorded in the Speed River for a species of *Paraleptophlebia*. Some penetrated to 30 cm (at T16), however, which Williams and Hynes also noted for their species. They thought this unusual because *Paraleptophlebia* has delicate gills, as does *Atalophlebioides*; these ought to prevent both taxa from penetrating interstitial spaces.

The Plecoptera appeared to penetrate only to 10–20 cm except during flood when they reached 20–30 cm. Williams (1984) noted that, in North America, stonefly nymphs have been commonly recorded to depths of 30 cm. In the Thomson River, Plecoptera were not common in the cores at any site.

Hydropsychid caddis flies (*Cheumatopsyche* spp.) were able to penetrate to 30 cm, despite being net-spinning filter feeders. Williams and Hynes (1974) recorded this genus to depths of 40 cm, especially the small instars. *Agapetus* sp. (Glossosomatidae) was mostly found in the surface 0–10 cm, which is understandable because it feeds on epilithic algae on the surface rocks (Chessman 1986), but it did occur down to 30 cm at T6.

The Chironomidae were abundant at all sites and always penetrated to 30 cm as did the Elmidae. Both these groups seem pre-adapted for an interstitial existence (Williams and Hynes 1974), having slender flexible bodies which can readily penetrate the bed sediments. This is borne out by the fact that during the flood at T6 these two groups (as well as other Diptera and the water mites) showed the highest percentage abundances at depths exceeding 10 cm. The Hydracarina and Oribatidae have hard exoskeletons which would enable them to force their way between sediment particles, another pre-adaptation noted by Williams and Hynes (1974) for interstitial existence. The other Diptera were only common at T6 and largely consisted of very thin (Ceratopogonidae) or slender (Tipulidae) forms. Simuliidae (*Austrosimulium victoriae* Roubaud) were found only at 0–10 cm, but have been reported from depths of 15–25 cm (Hynes *et al.* 1976) where porosities are high.

No comments can be made about seasonal variations in the patterns of vertical distribution. Williams and Hynes (1974) made a detailed study of this in the Speed River using monthly sets of samples and found marked changes during the course of 1 year. In the rivers of southern Australia, such study could prove extremely valuable, given the fact that discharge even in this relatively well watered part of the continent is known to be highly variable (Lake *et al.* 1985) and could thus lead to rapid variation in the mean depth of penetration of the river-bed by the benthic fauna.

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