Aust. J. Mar. Freshw. Res., 1986, **37**, 113–20

Estimates of Annual Production for Some Aquatic Insects from the La Trobe River, Victoria

R. Marchant

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

Abstract

Annual production was estimated by the size-frequency method for Ephemeroptera (*Tasmanocoenis tonnoiri*, two species of *Baetis*, *Atalonella* spp., *Atalophlebioides* sp.), Plecoptera (*Leptoperla* spp.) and Trichoptera (*Ecnomus* sp.) at four sites on the lowland section of the La Trobe River. Annual production (*P*) of individual ephemeropteran species (or genera) varied from 0·02 to 0·7 g m^{-2} while total annual production of this order at two sites was 0·7–1·5 g m^{-2}. Annual production of *Leptoperla* spp. was 0·03 g m^{-2} at one site while *Ecnomus* sp. averaged 2 g m^{-2} at two sites. Estimates of annual production were subject to an error of at least ±50%. Annual turnover ratios ($P/\bar{B}$; $\bar{B}$ is mean biomass) varied from 9 to 19 and were three to four times higher than published values for similar-sized macroinvertebrates in the temperate zone (generally <15°C mean annual habitat temperature). This probably resulted from the higher average temperatures (17–18°C) at most sites.

Introduction

It is now well accepted that estimates of secondary production are important for quantifying the roles, in particular the trophic roles, of aquatic invertebrates in streams and rivers (Benke *et al.* 1984). At present there are no published data for Australia on invertebrate production in rivers and few data on invertebrate production in lakes and ponds; there are, however, some unpublished data on secondary production in a small stream near Armidale, N.S.W. (Pidgeon 1978). This is in sharp contrast to the situation in the Northern Hemisphere, where a large body of data on secondary production now exists (Waters 1977; Benke *et al.* 1984), and it reflects the neglect of quantitative study of invertebrates from inland waters in Australia in general and from rivers in particular.

During a study of the distribution of benthic fauna along the lowland reach of the La Trobe River (38°10′S.,146°30′E.) (Marchant *et al.* 1984*a*), certain species of Ephemeroptera, Plecoptera and Trichoptera were sufficiently common to enable their life histories to be described (Marchant *et al.* 1984*b*). In this paper, data on life history and abundance of these taxa are combined to provide estimates of production for four species and one genus of Ephemeroptera, one genus of Plecoptera and one species of Trichoptera. Previous studies of invertebrate production in rivers have largely concentrated on taxa in these orders.

Study Area

Four sites (Nos 1, 5, 6 and 10) of the 10 sampled by Marchant *et al.* (1984*a*) in the lowland section of the La Trobe River were selected for study; these sites contained large populations of one or more of the chosen taxa. The river is 15–20 m wide and <1 m deep at each of these sites; the bottom varies from coarse sand (0·5–2 mm mean grain size) in the main channel to fine sand and silt (0·1–0·7 mm) along the banks. Mean water velocity ranges from 28 to

0067-1940/86/020113$02.00

56 cm s^{-1} in the main channel and from 9 to 12 cm s^{-1} at the bank, while mean monthly water temperature reaches a minimum of 8–15°C in July and a maximum of 21–24°C in January. Heated water (<25°C) enters the river just upstream of site 5, causing higher minimum mean temperatures (14–15°C) at this site and site 6 (about 2 km below site 5) than at sites 1 and 10 (8–10°C). The total distance between sites 1 and 10 is about 60 km; Marchant *et al.* (1984*a*) discuss the disturbances to the river and the changes in various water-quality variables that occur in this distance.

Methods

Sampling Procedure

Fifteen random samples were taken from the main channel and 15 from near the bank at each site, every 2 months between May 1979 and March 1981. An air-lift sampler was used, which sampled an area of 0·02 m^2; a catching net of 150-μm mesh was attached. Samples were preserved in the field in formalin and returned to the laboratory for identification and counting; further details are given by Marchant *et al.* (1984*a*).

Abundances of the various taxa were expressed as numbers per square metre. In order to combine data from the two habitats, the main channel was assumed to represent 90% of the river bed and the banks 10%; this was based on the bank zone occupying approximately 2 m (1 m on either bank) of the total width of the river (15–20 m). The 95% confidence limits (95% C.L.) of the mean abundances of a taxon on each sampling occasion were calculated after transforming the original counts (x) to $\log_{10}(x + 1)$ (Elliott 1977).

Calculation of Production

Production was estimated with the size-frequency method (Waters and Hokenstrom 1980), which assumes that the average size-frequency distribution of a taxon (expressed in numbers per square metre) approximates the survivorship of the average cohort. Production of an average cohort is the sum of the biomass losses between size classes, i.e. numbers lost multiplied by geometric mean weight; this sum is then multiplied by the number of size classes to give cohort production. To obtain an estimate of annual production, these values for cohort production must be corrected for the fraction of the year each taxon takes to complete development. This period is known as the cohort production interval (CPI) (Benke 1979). Thus, for a taxon with a CPI of 6 months, cohort production would be multiplied by two to give annual production. A factor of two would also apply to a univoltine taxon with a CPI of 6 months; in calculating annual production the duration of the CPI is the critical feature, not the voltinism.

Average CPIs and average size-frequency distributions for each taxon were obtained from data on their life histories given by Marchant *et al.* (1984*b*); in all cases these data extended over 2 years and over three to six cohorts. Dry weight of an individual in a particular size-class or instar of each taxon was estimated using regression equations relating body length or head width to dry weight (Smock 1980). This was preferable to actually weighing specimens as these had been in formalin and then 70% alcohol for long periods; these preservatives are known to cause loss of organic material (Downing 1984). The estimates of dry weight used by Smock (1980) presumably included the weight of the gut contents and are thus to some extent overestimates. However, such errors are probably small compared with the error in using regression estimates rather than actual measurements of dry weight. In addition, Marchant and Williams (1977) demonstrated that the overall error in the final estimate of production was much more strongly influenced by sampling errors in the field than by the smaller errors in the measurement of dry weight.

Results

Ephemeroptera

Annual production was calculated for five taxa (Table 1). *Tasmanocoenis tonnoiri* Lestage occurred at all sites on the lowland reach of the La Trobe River (Marchant *et al.* 1984*a*) but was most abundant at site 10, the site for which production was estimated. Production would have been less at all other sites provided the CPI for this species remained fairly constant; available size-frequency data suggested this was the case.

The two species of *Baetis* had largely disjunct distributions. The mean density of *Baetis* sp. 4 was one to two orders of magnitude greater at site 1 than at any other site, whereas *Baetis* sp. 5 was more widespread but most abundant at site 10. Thus the estimates of their

Table 1. Average abundance of nymphs per square metre in each size class (the average cohort) and annual production estimates (P) for Ephemeroptera and Plecoptera at two sites on the La Trobe River
Mean individual dry weight, mean nymph density (N), mean biomass ($\bar{B}$), mean cohort production interval (CPI) and annual turnover ratio ($P/\bar{B}$) are also given

Total length (mm)	Average abundance (No. m^{-2})	Mean individual dry wt (mg)	N (No. m^{-2})	$\bar{B}$ (mg m^{-2})	CPI (months)	Annual P (mg m^{-2})	Annual $P/\bar{B}$
		Ephemeroptera					
		Tasmanocoenis tonnoiri at site 10					
0·5	706	0·001					
1·5	848	0·02					
2·5	118	0·08	1722	35·4	5	657·8	18·6
3·5	46	0·18					
4·5	4	0·35					
5·5	0·3	0·52					
		Baetis sp. 4 at site 1					
0·9	85	0·003					
2·2	77	0·04					
3·4	30	0·17	204	14·1	5	202·8	14·4
4·7	11	0·46					
5·9	0·5	0·99					
7·2	—	—					
		Baetis sp. 5 at site 10					
0·9	33	0·003					
2·2	20	0·04					
3·4	6	0·17	60	2·5	9	22·4	9·1
4·7	1	0·46					
5·9	0·2	0·99					
7·2	—	—					
		Atalonella spp. at site 1					
0·9	478	0·006					
2·2	284	0·06					
3·4	44	0·23	847	56·9	7	688·6	12·1
4·7	34	0·57					
5·9	6	1·12					
7·2	0·5	1·94					
		Atalophlebioides sp. 4 at site 1					
0·9	879	0·006					
2·2	267	0·06					
3·4	75	0·23	1251	58·1	7	641·6	11·0
4·7	27	0·57					
5·9	3	1·12					
7·2	—	—					
		Plecoptera					
		Leptoperla spp. at site 10					
1	2	0·002					
2	7	0·024					
3	2	0·095					
4	1	0·25					
5	0·3	0·54	13	2·7	6	30·5	11·4
6	0·3	1·00					
7	0·3	1·68					
8	0·3	2·65					
9	0·06	3·95					

production (Table 1) are probably maximal values for the lowland stretch of the La Trobe River. The two species differed fairly markedly in their CPIs and annual turnover ratios. It seems unlikely that this was due to the somewhat warmer temperatures at site 10 (6072 degree days >0°C per year based on continuous records for 2 years) than at site 1 (4810 degree days) (Marchant *et al.* 1984*b*); if temperature had been an important factor, the shorter CPI and higher turnover ratio should have occurred at site 10. Also, the difference between the mean CPIs of the two species is greater than shown in Table 1. Marchant *et al.* (1984*b*) concluded that *Baetis* sp. 4 was at least bivoltine and probably multivoltine. However, its mean CPI was calculated assuming the species was bivoltine, as there were insufficient data to determine the degree of multivoltinism.

Fourteen species of Leptophlebiidae occurred at site 1 (Marchant *et al.* 1984*c*) but three dominated (*Atalonella* spp. 2 and 4; *Atalophlebioides* sp. 4) and together constituted 93% of the total. Production was estimated for these two genera separately. Large numbers of very small leptophlebiid nymphs, which could not be identified to any of the 14 species, also occurred at certain times; these were added to the smallest size class of each genus in proportion to the mean abundance of each genus, i.e. 40% to *Atalonella* and 60% to *Atalophlebioides*. The results were considered to be the average cohorts (Table 1) for the two taxa. Abundances of the two genera were lower at other sites, suggesting production was lower also.

Mean dry weight of an individual in each size class was estimated for *T. tonnoiri* and the two *Baetis* spp. from regressions of weight on length for Caenidae (*Caenis* sp.) and Baetidae (*Baetis* sp.), respectively (Smock 1980). Smock did not include any Leptophlebiidae in his study and the dry weights for the two taxa in this family were calculated from his regression for the Ephemeroptera as a whole derived from data for eight species. To gain some idea of the possible bias in this procedure, dry weight was recalculated for the two leptophlebiid taxa using the regressions that gave the maximum and minimum dry weights for a given body length for Smock's eight species. This resulted in values for production that varied by ±30–40% from those in Table 1. As these maximum and minimum values were based on species that were distinctly larger or smaller than the Leptophlebiidae, the probable bias in using the general ephemeropteran regression appears small.

Plecoptera

Two species, *Leptoperla primitiva* McLellan and *L. neboissi* McLellan, occurred at a number of sites in the lowland reach of the La Trobe River. They were most abundant at site 10 where production (Table 1) was calculated; only one other species of Plecoptera occurred at this site but it was very rare. The smallest instars of the two species could not be distinguished from each other and thus the mean densities of the two species were summed to produce the average cohort. At site 10 *L. primitiva* was approximately twice as abundant as *L. neboissi*. The CPI appeared to be similar at other sites (Marchant *et al.* 1984*b*), but as densities were lower so too presumably was production.

Dry weight was estimated from body length using a general regression equation for Plecoptera (Smock 1980) based on data from eight species. If maximum and minimum dry weights (from the extreme regressions) are substituted, production varies by ±30%.

Trichoptera

Ecnomus sp. was most abundant at sites 5 and 6, the sites at which its production was calculated (Table 2). At other sites its production would probably always have been less as densities were much lower. Mean density of larvae at site 5 was half that at site 6 (Table 2). However, mean biomass was higher at site 5, largely as a result of higher densities in the largest instars, and the resulting estimates of production were similar. Turnover ratios were also similar at these two sites, which had more or less the same annual temperature regime (6708 degree days at site 5, 6720 degree days at site 6; Marchant *et al.* 1984*b*).

Dry weight for each instar of *Ecnomus* sp. was estimated from a general regression relating dry weight to head capsule width for Trichoptera (Smock 1980) based on data from seven species. Head capsule widths for each instar of *Ecnomus* sp. are given by Marchant *et al.* (1984*b*). If maximum and minimum dry weights from Smock's data are substituted, production varies by ±20–40%.

Confidence Limits of Estimates

The 95% C.L. for the mean densities (Tables 1 and 2) of the various taxa on each sampling occasion varied from an average of 40% for *Ecnomus* sp. and *Baetis* spp. to 60% for *T. tonnoiri* and *Atalophlebioides* sp. Confidence limits were not available for the *Leptoperla* spp., but as the densities of this taxon were lower than those of the other taxa percentage error was probably higher. Thus the production estimates are probably subject to at least an error of ±50%.

Table 2. Average abundance of larvae per square metre in each instar (the average cohort) and annual production estimates (*P*) for *Ecnomus* sp. (Trichoptera) at two sites on the La Trobe River
Mean individual dry weights, mean density (N), mean biomass ($\bar{B}$), mean cohort production interval (CPI) and annual turnover ratio ($P/\bar{B}$) are also given

Instar	Average abundance (No. m^{-2})	Mean individual dry wt (mg)	N (No. m^{-2})	$\bar{B}$ (mg m^{-2})	CPI (months)	Annual P (mg m^{-2})	Annual $P/\bar{B}$
			Site 5				
1	322	0·02					
2	434	0·08					
3	176	0·22	1064	280·3	7	2396·4	8·6
4	96	0·86					
5	37	3·23					
			Site 6				
1	905	0·02					
2	771	0·08					
3	210	0·22	1924	183·0	7	1885·7	10·3
4	29	0·86					
5	10	3·23					

The uncertainties in calculating dry weight from Smock's (1980) regressions undoubtedly add to this error. But even the extreme values for dry weight, in the case of the Leptophlebiidae, increase total error only to ±70%, if the approximate formula for calculating the variance of production is applied (see Marchant and Williams 1977). It should be remembered that the estimates of production are the maximum rates likely to prevail in the La Trobe River because they were calculated for sites where the selected species were most abundant.

Krueger and Martin (1980) have developed a technique for computing the 95% C.L. for estimates of production calculated by the size-frequency method. This technique was not used as it relies only on estimates of the variance of the density in each size class and does not account for systematic errors in estimating the mean CPI or the mean weight of an individual. In addition, the fact that the size-frequency method for estimating production is itself an approximation does not seem to justify the setting of such definite confidence limits.

Discussion

Errors in Production Estimates

The original proponents of the size-frequency method for calculating production (Hynes and Coleman 1968; Hamilton 1969) considered it was accurate to an order of magnitude when applied to the entire benthos. However, since then others (Waters 1977) have compared estimates of production for single species obtained by this method with those from other methods of calculation in which discrete cohorts are followed, and found close correspondence between the values. As a result the size-frequency method is now considered nearly as accurate as these other methods (Krueger and Martin 1980). However, all production studies of benthic invertebrates suffer to a greater or lesser degree from errors introduced in the actual sampling of the fauna.

In this study the air-lift sampler extracted benthic material from an area of 0·02 m^2, but was probably only effective in doing so for a few centimetres into the substratum. Drake and Elliott (1982) showed that a similar apparatus could only be considered as sampling quantitatively down to 3 cm below the surface of fine gravel (2–4 mm), a substratum that is somewhat coarser than the sand that dominates the lower reach of the La Trobe River. Marchant *et al.* (1984*a*) found that the fauna extended to at least 30 cm below the surface of the substratum in this section of the river, but no Ephemeroptera or Trichoptera were found below 5 cm (based on one set of samples taken in summer). However, Williams and Hynes (1974) showed that Caenidae at certain seasons could penetrate to 70 cm; the more delicate Leptophlebiidae, on the other hand, were more or less confined to the surface of the substratum. Examination of changes in density of the species considered in this paper (Marchant *et al.* 1984*b*) indicated no large unexpected or irregular increases that could be due to recruitment to the surface from deep in the sediment. Thus these species either have a constant pattern of vertical distribution through their life cycles, which is contrary to the seasonal variation in such distributions for aquatic insects clearly shown by Williams and Hynes (1974), or only a minority of the population of these particular species exists at depths >3 cm during most of the life cycle.

Another common problem with many production studies is the absence or gross underestimation of the density of the smallest instars. Tables 1 and 2 indicate three instances out of a possible eight (*T. tonnoiri*, *Leptoperla* spp. and *Ecnomus* sp. at site 5) where mean densities of the smallest size class are lower than those of the next smallest size class. Thus the problem has not been solved completely by using a fine mesh (150 μm) but any such underestimates are probably smaller than in many previous studies. Low densities in the smallest size classes may also be due to the nymphs and larvae spending only short periods at these sizes and thus occurring less frequently than those in larger more long-lived size classes. In my calculations negative values resulting from such non-linear growth were not excluded as they were by Benke and Wallace (1980); production estimates were reduced by $<2\%$ by this procedure. Hamilton (1969) showed such non-linear growth did not seriously affect values for production calculated by the size-frequency method.

On account of the above problems it seems likely that the estimates of production (Tables 1 and 2) have at least an error of $\pm 50\%$ (the 95% C.L. for density) and a possible maximum error of an order of magnitude. Many estimates of benthic invertebrate production are no more accurate, when examined closely, because they suffer from similar shortcomings especially in the sampling of the fauna. In the absence of other data on production for Australia, the estimates (Tables 1 and 2) are valuable and can be readily compared with estimates from elsewhere as the size-frequency technique has been widely used.

Comparison of Production Estimates

The total annual production of the Ephemeroptera varied from 0·7 g m^{-2} at site 10 to 1·5 g m^{-2} at site 1 (assuming little additional production occurred among the rare species at these sites omitted from the calculations; these rare species formed $<5\%$ of the total ephemeropteran population at both sites). Additional data for *T. tonnoiri* (Marchant *et al.* 1984*c*) from the lowland sites on the Thomson River, the catchment of which is adjacent to that of the La Trobe River, give an estimate of annual production of 3·7 g m^{-2} ($P/\bar{B} = 18 \cdot 4$; $N = 1 \cdot 3 \times 10^4$ nymphs m^{-2}). Total production of Ephemeroptera in this river would thus be quite a bit larger than that measured for the La Trobe River. The thermal regime at the two sites on the Thomson River differed little from that at site 10.

At two sites on the Satilla River in southern U.S.A. (approximately 31°N. latitude) Benke *et al.* (1984) measured annual production (using the size-frequency technique) of the total fauna on snags along the river bank. The temperature regime at these two sites was quite similar to that in the lower section of the La Trobe River, but was somewhat warmer (25–30°C on average) during the summer months. Annual production of the Ephemeroptera varied from 0·6 to 1·2 g m^{-2} with $P/\bar{B}$ ratios of 11–14; these values are very similar to those from the La Trobe River. However, production levels for the Plecoptera of about 1 g m^{-2} and those for the Trichoptera of 12–26 g m^{-2} (with $P/\bar{B}$ ratios of 6·2–7·5) are substantially higher. (*Leptoperla* and *Ecnomus* were the numerically dominant members of their respective orders at the sites studied in the La Trobe River.)

The snags occupied only about 5% of the area of the Satilla River; no Ephemeroptera or Plecoptera and few Trichoptera were found in the main channel or back-waters, which formed most of the area of the river bed. Thus, if the production values are quoted in terms of the area of the whole river (as are the values from the La Trobe River) then the estimates are reduced: for the Ephemeroptera to 0·03–0·06 g m^{-2}, for the Trichoptera to 0·6–1·3 g m^{-2} and for the Plecoptera to 0·05 g m^{-2}. These reduced estimates, except those for the Ephemeroptera, are now similar to the values estimated in the La Trobe River.

Waters (1977) in his review of secondary production summarized available data for individual species in the Ephemeroptera, Trichoptera and Plecoptera. These data indicate that the values recorded in the La Trobe River are within the range of previous measurements, but that the annual turnover ratios ($P/\bar{B}$) are generally two to three times higher.

Banse and Mosher (1980) showed there was a strong inverse relation between the annual $P/\bar{B}$ ratio and mass at maturity for a range of (largely aquatic) invertebrates from the temperate zone, i.e. mean annual habitat temperature of 5–20°C. Turnover ratios calculated from their regression equation for the species in this paper are three to four times lower than the ratios observed (Tables 1 and 2). The average temperatures at sites 5, 6 and 10 were 17–18°C; that at site 1 was 13°C. Only two of the thirty-one species in Banse and Mosher's regression were studied at sites with average temperatures >17°C and none of the aquatic insects included had $P/\bar{B}$ values >5, i.e. most had life spans exceeding a year. Thus it seems that their equation is no longer valid when data from this study and from the much more extensive study of Benke *et al.* (1984) are considered (the mean annual temperature in the Satilla River was about 20°C).

The estimates of production also vary according to the probable diet of each species. *Ecnomus* sp. is a generalist (Chessman 1982) that eats both benthic algae and zooplankton. As sites 5 and 6 are immediately below an impounded section of the river (Marchant *et al.* 1984*a*), where zooplankton would be abundant, the high relative levels of production of this taxon are not surprising. The high mean water temperatures in winter at these sites compared with sites 1 and 10 also may have promoted growth better. *Baetis* and *Leptoperla* (scrapers) (Chessman 1982) have the lowest levels of production of the species studied. Chessman (1982) found very low levels of benthic primary production in the La Trobe River, which he attributed to the high turbidity of the water. *T. tonnoiri* (a gatherer) (Chessman 1982) and *Atalonella* spp. (shredders) have intermediate levels of production, as does *Atalophlebioides* sp., which, however, is a scraper. Thus the relative levels of production of the taxa reflect to some extent the availability of the major items in the diet.

Acknowledgment

Data used in this paper were collected during a study financed by the State Electricity Commission of Victoria. I am very grateful to the Commission for support and information.

References

Banse, K., and Mosher, S. (1980). Adult body mass and annual production/biomass relationships of field populations. *Ecol. Monogr.* **50**, 335–79.

Benke, A. C. (1979). A modification of the Hynes method for estimating secondary production with particular significance for multivoltine populations. *Limnol. Oceanogr.* **24**, 168–71.

Benke, A. C., Van Arsdall, T. C., Gillespie, D. M., and Parrish, F. K. (1984). Invertebrate productivity in a subtropical blackwater river: the importance of habitat and life history. *Ecol. Monogr.* **54**, 25–63.

Benke, A. C., and Wallace, J. B. (1980). Trophic basis of production among net-spinning caddisflies in a southern Appalachian stream. *Ecology* **61**, 108–18.

Chessman, B. C. (1982). Algal and functional ecology. State Electricity Commission of Victoria, Latrobe Valley Water Resources Biological Studies, Vol. 3.

Downing, J. A. (1984). Sampling the benthos of standing waters. In 'A Manual on Methods for the Assessment of Secondary Production in Fresh Waters'. (Eds J. A. Downing and F. H. Rigler.) pp. 87–130. (Blackwell Scientific Publications: Oxford.)

Drake, C. M., and Elliott, J. M. (1982). A comparative study of three airlift samplers used for sampling benthic macroinvertebrates in rivers. *Freshwater Biol.* **12**, 511–33.

Elliott, J. M. (1977). 'Some Methods for Statistical Analysis of Samples of Benthic Invertebrates.' Scientific Publication No. 25. (Freshwater Biological Association: Cumbria.)

Hamilton, A. L. (1969). On estimating annual production. *Limnol. Oceanogr.* **14**, 771–82.

Hynes, H. B. N., and Coleman, M. J. (1968). A simple method of assessing the annual production of stream benthos. *Limnol. Oceanogr.* **13**, 569–75.

Krueger, C. C., and Martin, F. B. (1980). Computation of confidence intervals for the size-frequency (Hynes) method of estimating secondary production. *Limnol. Oceanogr.* **25**, 773–7.

Marchant, R., Mitchell, P., and Norris, R. (1984*a*). Distribution of benthic invertebrates along a disturbed section of the La Trobe River, Victoria: an analysis based on numerical classification. *Aust. J. Mar. Freshw. Res.* **35**, 355–74.

Marchant, R., Graesser, A., Metzeling, L., Mitchell, P., Norris, R., and Suter, P. (1984*b*). Life histories of some benthic insects from the La Trobe River, Victoria. *Aust. J. Mar. Freshw. Res.* **35**, 793–806.

Marchant, R., Mitchell, P., and Norris, R. (1983*c*). A distribution list for the aquatic invertebrates in the lowland region of the La Trobe River, Victoria. *Occas. Pap. Mus. Victoria* **1**, 63–79.

Marchant, R., and Williams, W. D. (1977). Population dynamics and production of a brine shrimp, *Parartemia zietziana* Sayce (Crustacea : Anostraca), in two salt lakes in western Victoria, Australia. *Aust. J. Mar. Freshw. Res.* **28**, 417–38.

Pidgeon, R. W. J. (1978). Energy flow in a small stream community: an evaluation of the effects of different riparian vegetation. Ph.D. Thesis, University of New England.

Smock, L. A. (1980). Relationships between body size and biomass of aquatic insects. *Freshwater Biol.* **10**, 375–83.

Waters, T. F. (1977). Secondary production in inland waters. *Adv. Ecol. Res.* **10**, 91–164.

Waters, T. F., and Hokenstrom, J. C. (1980). Annual production and drift of the stream amphipod *Gammarus pseudolimnaeus* in Valley Creek, Minnesota. *Limnol. Oceanogr.* **25**, 700–10.

Williams, D. D., and Hynes, H. B. N. (1974). The occurrence of benthos deep in the substratum of a stream. *Freshwater Biol.* **4**, 233–56.

Manuscript received 22 November 1984, accepted 11 June 1985