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Secondary production of a stream metazoan community: Does the meiofauna make a difference?

Abstract—The benthic communities of streams contain invertebrates of a wide range of body size and from many taxa. Owing mainly to methodological problems, however, the contribution of smaller and more obscure metazoans to community structure and dynamics, including production, is poorly known compared with that of larger size fractions and, particularly, insects and macrocrustaceans. Based on a monthly survey of a first-order, acidic English stream, we used the size–frequency method to estimate annual production of the whole metazoan benthos (down to organisms retained on a 42-μm mesh and being as taxonomically inclusive as possible). Mean total secondary production (5.22 g dry weight m^{-2} yr^{-1}) was low, presumably mainly due to the stream's acidity. About 15% (0.76 g m^{-2} yr^{-1}) of this total production, however, was contributed by the permanent meiofauna (species always small enough to pass through a 500-μm mesh, and mainly made up of ostracods and copepods but also including rotifers, microturbellarians, and others). By estimating separately production from the macrofaunal and meiofaunal net fractions (500 μm and 42–500 μm, respectively), we found that about 51% of total production could be accounted for by the permanent and temporary meiofauna together, the latter being defined as organisms that potentially grow into the macrofaunal size class and here consisting primarily of oligochaetes, chironomids, and plecopterans. This study points to the potentially substantial underestimation of production arising from the problems of assessing the meiofauna, including the former use of coarse-meshed (e.g., 500 μm) sampling devices, the requirement for live sorting of many soft-bodied taxa, and other difficulties of counting and identifying less well known groups.

Secondary production, defined as the amount of tissue elaborated per unit time and area, regardless of its fate, constitutes one of the major pathways of energy flow in communities. Freshwater production studies have been based mainly on the larger size classes of single species (e.g., Iverson 1988; Benke and Wallace 1997), with estimates for entire communities being rare (Krueger and Waters 1983; Strayer and Likens 1986; Benke et al. 1988). Benke et al. (1988) attributed this largely to the cost, in terms of time and money, of collecting and sorting the samples required. In addition, the contribution to production of the smaller metazoans or meiofauna (invertebrates passing through a mesh of 500 μm but retained on one of 42 μm, and many of them requiring specialized methods and taxonomic skills) has remained speculative (Hakenkamp et al. 2002).

Despite their small size, meiofaunal invertebrates have a high rate of turnover and generally short generation times and so potentially contribute significantly to overall community production. At present, we know that meiofaunal species are important intermediates in stream food webs (Schmid-Araya et al. 2002 and references therein). The meiofauna mostly live interstitially, although some are epibenthic, reproduce rapidly, and are important prey for the smallest instars of what ultimately become large invertebrate predators (Schmid-Araya et al. 2002). In addition, the production of these underestimated invertebrates may further account for the Allen paradox (after Allen 1951), which refers to the apparent discrepancy in some streams between the calculated supply of prey required to support fish production and independent estimates of the density of that prey (O'Doherty 1985; Huryn 1996).

There have been few attempts to calculate the secondary production of the freshwater meiofauna. However, Strayer and Likens (1986) found that half of the benthic carbon assimilation at Mirror Lake was by invertebrates that would normally pass through a 250-μm sieve. Poff et al. (1993) found that the permanent meiofauna dominated energy flow in a sandy stream and accounted for 45% of estimated community respiration. In a stream in the Ottawa Valley with coarse substratum and dominated by insects, however, 80% of total production resulted from the growth of invertebrates between 1 and 10 mm in length, and only 3% from invertebrates $<$1 mm (Hakenkamp and Morin 2000).

Because generation times of meiofauna are short and reproduction continuous for much of the year, they lack the discrete cohorts that make the calculation of secondary production straightforward (Anderson et al. 1998). Further, growth rates are usually not known and cannot be used, therefore, to estimate production. In addition, Banse and Mosher (1980) noted the lack of published production to biomass (P/B) ratios for meiofaunal species, a conclusion that is still essentially true more than two decades later, although there have been notable additions (e.g., Strayer and Likens 1986). The most suitable method for estimating production, therefore, is the size–frequency method (Hynes and Coleman 1968), later modified by Hamilton (1969). If it is not possible to detect clear cohorts, the method approximates the survivorship of an average cohort (Benke and Wallace 1997) and has commonly been used in studies of community production (Krueger and Waters 1983; Iverson 1988; Lugthart and Wallace 1992; Benke and Wallace 1997).

We previously carried out a monthly survey of the metazoan benthos over 1 yr in a small stream and estimated density and biomass of both the macrofauna and the diverse and abundant meiofauna, including several taxonomically challenging groups of soft-bodied meiofauna that require live sorting and identification (Stead et al. 2003). Our principal aim here was to determine secondary production for the whole benthos over the same wide size range, including the macrofauna and both the permanent and temporary meiofauna. The permanent meiofauna comprises taxa that spend their entire life cycle within the meiofaunal size range (i.e., passing through a sieve of 500 μm but retained on one of 42 μm), while the temporary meiofauna (typically insects and oligochaetes) grow beyond this size range. In addition, we compared the relative contribution of the different size classes within and between taxonomic groups. Overall, we sought to assess the contribution to production of small and obscure metazoans and also the extent to which studies that exclude them may be underestimating community processes.

Methods—Benthic sampling: Lone Oak is an acidic and fishless headwater of the River Medway in the Ashdown Forest of southeast England (51°04′33″N, 0°06′12″E). The substratum is a mixture of particle sizes from gravel to large cobbles, and the stream is underlain by sandstone bedrock with patches of Wadhurst clay. Channel width and mean depth are 2–4 m and 0.05–0.20 m, respectively, temperature ranges between 4°C and 15°C and pH between about 4 (in acidic episodes in winter) and briefly up to about 7 in summer. The immediate riparian vegetation is woodland dominated by Oak (*Quercus robur*) and Beech (*Fagus sylvatica*), that shades the stream and provides a copious source of allochthonous litter. The remainder of the catchment is dominated by acidic heathland. Monthly benthic samples of all invertebrates larger than 42 μm were collected between March 1999 and April 2000 inclusive (Stead et al. 2003), although our production estimates are based on the 12-month period March 1999 to February 2000 only. Except for September 1999, at least eight (maximum 15) randomly dispersed Hess samples (mesh size 42 μm) were collected from the stream on each occasion. This is a quantitative sampler, effective to a sediment depth of about 5 cm. Only three sample units were processed in September 1999 due to excessive fine particulate organic matter in the samples making sorting extremely time consuming. In the laboratory, samples were passed through a 500-μm sieve and then one of 42 μm and thus were separated into meiofaunal and macrofaunal fractions. To account for the soft-bodied meiofauna that are destroyed when preserved, a proportion of the meiofaunal samples was sorted live. All invertebrates were identified and measured. Body dimensions were converted to dry weight using published length–dry weight regressions, and mean biomass ranged from 0.006 to 8,000 μg dry weight. Survey, field, and laboratory methods and dry weight calculations are described in detail in Stead et al. (2003) along with the published regressions used.

Calculation of secondary production: Production was calculated by the size–frequency method of Hynes and Coleman (1968), applying the modifications recommended by Hamilton (1969) and Benke (1979). For practical purposes, individuals were lumped into groups by genus, family, or order and separate calculations performed for each group. These groupings increased the accuracy of the estimates by allowing for differences in maximum attainable body size and generation time between taxa (Hamilton 1969; Benke 1979). After Benke (1979), each group was allocated a cohort production interval (CPI: the generation time minus any time not contributing to benthic production, such as a terrestrial adult phase), calculated from generation times gathered from the literature or other sources (Web Appendix 1 at http://www.aslo.org/lo/toc/vol_50/issue_1/0398a1.pdf). If a range of generation times was available in the literature, then that value corresponding to the appropriate temperature range in the stream was selected. If the quoted generation times were within the correct temperature range for Lone Oak, the minimum temperature and, hence, the maximum generation time and vice versa were selected to produce a range of possible production rates. Production increases with temperature, however, and many quoted estimates of generation time are for organisms kept at 20°C, possibly resulting in an overestimation of production in the stream where temperatures ranged from 4°C to 15°C over the sampling period.

Each group was then divided into 10 equal size classes a priori and production calculated, any apparently negative values for production in any size class being discarded following the method of Hamilton (1969). Since the individual body sizes of all the taxa were known, mass classes were used (Hamilton 1969), rather than length classes as in the original method of Hynes and Coleman (1968). Finally, total production was multiplied by 365/CPI to correct for the number of generations per year. Three calculations of production were made for each group and for the total benthos: (1) one based on the sample across the whole size range, (2) one based on the 500-μm net fraction (i.e., the macrofauna), and (3) one based on the 42–500-μm net fraction (the meiofauna).

Results—Total production, summary: For the period March 1999 to February 2000, mean total production at Lone Oak was 5.22 g dry weight m^{-2} yr^{-1}, the estimate ranging from 4.65 to 5.79 g dry weight m^{-2} yr^{-1} depending on assumptions about generation times (Table 1). The corresponding standing biomass was 0.69 g dry weight m^{-2}.

Insects contributed 47% (2.45 g m^{-2} yr^{-1}) of overall production compared with noninsect taxa with 53% (2.76 g m^{-2} yr^{-1}) (Table 1). The permanent meiofauna, i.e., microcrustacea, Rotifera, Nematoda, Microturbellaria, and Gastrotricha, contributed 15% (0.76 g m^{-2} yr^{-1}, range 0.55 to 0.97) of annual production, although accounting for just 3% of the standing biomass (Table 1).

By calculating production for the two net fractions separately, it was estimated that meiofaunal production was similar (51% of the total of the two) to that of the macrofauna (2.68 and 2.54 g m^{-2} yr^{-1}, respectively; Table 1). Most meiofaunal production was contributed by noninsects.

Between-taxon comparison of production: The five most productive taxa across the entire size spectrum, together contributing 85% of total production, were the Oligochaeta, Plecoptera, Chironomidae, Trichoptera, and Ostracoda (Table

Table 1. Standing biomass and production (dry weight) values for the metazoan community at Lone Oak between March 1999 and February 2000. Categories for comparison are as follows: (1) insects and noninsects, (2) permanent meiofauna and all other remaining taxa, (3) macrofauna and meiofauna (each further subdivided into insects and noninsects). Percentage of total is given in parentheses. Mean, minimum, and maximum figures are those calculated from the range of published generation times, i.e., maximum production rates are calculated from the minimum generation time and vice versa. Estimates of production in the first four rows are based on the entire sample, whereas those in the following six rows result from the two net fractions separately (i.e., 500 μm and 42–500 μm).

Metazoan community*	Production (g m^{-2} yr^{-1}) Mean (%)	Min	Max	Standing biomass (g m^{-2}) (%)
1				
Insects	2.45 (47)	2.10	2.81	0.31 (45)
Noninsects	2.76 (53)	2.55	2.97	0.38 (55)
2				
Permanent meiofauna	0.76 (15)	0.55	0.97	0.02 (3)
3				
Macrofauna and temporary meiofauna	4.46 (85)	4.10	4.81	0.66 (97)
Macrofauna (retained on 500 μm sieve)	2.54 (49)	2.22	2.86	0.33 (48)
Insects	2.22 (43)	1.90	2.54	0.28 (41)
Noninsects	0.32 (6)	0.32	0.32	0.05 (7)
Meiofauna (passing through 500 μm sieve)	2.68 (51)	2.43	2.92	0.36 (52)
Insects	0.24 (4)	0.20	0.27	0.02 (3)
Noninsects	2.44 (47)	2.23	2.65	0.33 (48)
Total	5.22	4.65	5.79	0.69

* Insects + noninsects = permanent meiofauna + macrofauna and temporary meiofauna = macrofauna >500 μm + meiofauna <500 μm = total. Macrofauna >500 μm = insects + noninsects. Meiofauna <500 μm = insects + noninsects.

2). One of these taxa, the Ostracoda, belonged to the permanent meiofauna, while the first four also had the greatest standing biomass.

Based on estimates from the two net fractions separately, the five most productive taxa in the macrofaunal size class were the Plecoptera, Chironomidae, Trichoptera, Oligochaeta, and Tipulidae (Table 3, top). The five most productive taxa within the meiofauna were the Oligochaeta, Ostracoda, Copepoda, Nematoda, and Chironomidae, these taxa together contributing 96% of the meiofaunal production (Table 3, bottom).

P/B ratio varied widely between taxa, from 1 to 27 for the insects and oligochaetes to greater than 300 for some rotifers (Web Appendix 2 at http:/www.aslo.org/lo/toc/vol_50/issue_1/0398a2.pdf).

Within-taxon production: The seven most productive taxa in the macrofaunal net fraction (Plecoptera to Ephemeroptera in Table 3, top) also appeared as temporary members of the meiofauna (Table 3, bottom). Only in the single noninsect taxon among them, the Oligochaeta, was most production attributable to the meiofaunal fraction, although this was the most productive taxon in the stream overall.

Discussion—Even by including metazoans over a wide range of body size and taking a taxonomically highly inclusive approach, mean total secondary production (5.22 g dry weight m^{-2} yr^{-1}) at Lone Oak was fairly low when compared with other streams. Previous studies have shown community production values across different streams to vary between 0.6 and 612 g m^{-2} yr^{-1} (Hamilton 1969; Strayer and Likens 1986; Iverson 1988; Benke 1993). The summary of Benke (1993) showed that streams with a very high community productivity (more than about 50 g dry weight m^{-2} yr^{-1}) were mostly organically enriched. Further, although most of these studies took account of all or most of the macroinvertebrate community, the meiofauna was not explicitly included yet accounted for about half of the already meager total at Lone Oak.

Productivity evidently varies considerably between streams (Benke et al. 1988; Benke 1993), and there are several possible reasons for the low values found at Lone Oak. Most probably, low production was due to the profoundly acidic nature of the stream. This result was not unexpected since acid streams in Europe and North America generally have a lower diversity and abundance of macroinvertebrates and meiofauna than equivalent circumneutral systems (e.g., Rundle and Hildrew 1990), while secondary production is also usually low (Krueger and Waters 1983; Griffith et al. 1994). Underlying this may be the fact that decomposition is slow in acid waters and microbial activity inhibited, probably accounting for slow growth in detritivorous animals (e.g., Groom and Hildrew 1989; Dangles et al. 2004).

Clearly, there could also be methodological problems. The lack of clear population cohorts and known individual growth rates renders production estimates somewhat more difficult, and the size–frequency method was the only suitable approach. However, separating the community into similar groups prior to calculations and correcting for the cohort production interval (after Benke 1979) compensated for the problems intrinsic to the method. With these modifications to the original procedure of Hynes and Coleman (1968), the

Table 2. Standing biomass and production (dry weight) estimates for the whole metazoan community (i.e., based on the entire sample) from March 1999 to February 2000 inclusive. Mean, minimum, and maximum production estimates are given (*see* Table 1). Taxa have been ordered according to their mean production.

	Production ($g\ m^{-2}\ yr^{-1}$)			Standing biomass ($g\ m^{-2}$)
	Mean	Min	Max	
Oligochaeta	2.00	2.00	2.00	0.36
Plecoptera	0.85	0.80	0.90	0.12
Diptera: Chironomidae	0.85	0.60	1.09	0.06
Trichoptera	0.46	0.46	0.46	0.07
Ostracoda	0.27	0.20	0.33	0.004
Copepoda	0.24	0.13	0.35	0.01
Nematoda	0.18	0.15	0.21	0.01
Diptera: Simuliidae	0.12	0.05	0.18	0.01
Diptera: Tipulidae	0.11	0.11	0.11	0.02
Ephemeroptera	0.07	0.07	0.07	0.02
Niphargus	0.05	0.05	0.05	0.003
Rotifera	0.02	0.020	0.03	0.0001
Microturbellaria	0.003	0.001	0.005	0.00001
Bivalvia	0.0005	0.0005	0.0005	0.0001
Collembola	0.0005	0.0005	0.0005	0.00003
Asellus	0.0003	0.0003	0.0003	0.0001
Megaloptera	0.0001	0.0001	0.0001	0.00003
Cladocera	0.00007	0.00007	0.0001	0.000004
Tardigrada	0.00005	0.00001	0.00009	0.000004
Gastrotricha	0.00001	0.000008	0.00001	0.0000001
Total	5.22	4.65	5.79	0.69

size–frequency method gives estimates consistent with other techniques (Krueger and Martin 1980). Further, we have chosen the most appropriate estimates available, from the published and unpublished records of ourselves and others, of the generation time of stream-dwelling invertebrates from acid streams in the cool temperate zone (Web Appendix 1).

The most intriguing result of this study is the high proportion of the total secondary production contributed by the meiofauna, which has rarely been distinguished before. Owing partly to the use of net meshes greater than 42 μm, some previous studies of stream production may have underestimated somewhat the meiofaunal fraction of the production of familiar benthic insects and crustaceans, while the difficulties of quantifying and identifying several taxa in the permanent meiofauna means that they have not usually been included in production estimates. Banse and Mosher (1980) highlighted the fact that estimates of P/B ratio for the small benthic invertebrates were lacking. This study provides P/B ratios for all of the major freshwater permanent meiofaunal taxa and shows that these ratios, although quite wide ranging, are generally *much* higher than those of the macrofauna, reflecting their rapid turnover. Thus, taxa in the permanent meiofauna contributed only 3% of biomass but 15% of secondary production and had an overall P/B ratio of 38, compared with an overall P/B ratio for the whole community of about 7.6.

Overall, the most productive taxa were the Oligochaeta, Plecoptera, Chironomidae, Trichoptera, and Ostracoda. Most species in the three insect taxa, and many oligochaetes, appear only temporarily in the meiofaunal size fraction. Krueger and Waters (1983) also found that these were among the most productive taxa in their study of macroinvertebrate production in streams of varying alkalinity. It is notable, however, that the Ostracoda was among the five most productive taxa and were taken only in the meiofaunal fraction. Hakenkamp and Morin (2000) claimed that the meiofauna is more productive when dominated by permanent rather than temporary taxa because the production of insects (temporary meiofauna) is primarily in the larger instars taken in the macrofaunal fraction. At Lone Oak, however, the permanent meiofauna contributed 15% of community production and just 3% of mean biomass, despite the fact that it included some of the most numerous taxa (Stead et al. 2003). Strayer (1985) found that microbenthic and permanently meiobenthic animals contributed 25% of the biomass and 35% of the production of the zoobenthos in Mirror Lake, a considerably higher contribution than the permanent meiofauna at Lone Oak.

Body size distributions at Lone Oak showed that noninsects were just as abundant as the insects in terms of numbers and biomass, in different size classes and at different times of the year (Stead 2002). The production estimates have shown that the insects and oligochaetes were the most productive groups in this stream. Moreover, much of the secondary production of oligochaetes resided in the meiofaunal size range (Stead et al. 2003). Within the insects, in contrast, the macrofauna was the most productive size fraction. This is not surprising since the Trichoptera and some Plecoptera, in particular, are quite large and abundant in the macrofaunal size fraction (Stead et al. 2003).

Lugthart and Wallace (1992) calculated the production of insect and noninsect taxa for streams in the Coweeta catchment, North Carolina, using the size–frequency method. They showed that the insects contributed between 81% and 86% of the macrofaunal production (7.61 and 11.34 $g\ m^{-2}\ yr^{-1}$, respectively) for different streams. Similarly, insects at

Table 3. Standing biomass and production estimates for all taxa based on the two net fractions separately. Mean, minimum, and maximum production estimates are given (*see Table 1*). Taxa have been ordered according to mean production.

	Production (g m^{-2} yr^{-1})			Standing biomass (g m^{-2})
	Mean	Min	Max	
Macrofauna (retained on a 500-μm sieve)				
Plecoptera	0.77	0.72	0.82	0.11
Diptera: Chironomidae	0.70	0.48	0.92	0.05
Trichoptera	0.46	0.46	0.46	0.07
Oligochaeta	0.28	0.28	0.28	0.04
Diptera: Tipulidae	0.11	0.11	0.11	0.02
Diptera: Simuliidae	0.11	0.05	0.16	0.01
Ephemeroptera	0.07	0.07	0.07	0.02
Niphargus	0.05	0.05	0.05	0.003
Bivalvia	0.0005	0.0005	0.0005	0.0001
Asellus	0.0003	0.0003	0.0003	0.0001
Megaloptera	0.0001	0.0001	0.0001	0.00003
Total	2.54	2.22	2.86	0.33
Meiofauna (passing through a 500-μm sieve)				
Oligochaeta	1.73	1.73	1.73	0.32
Ostracoda	0.27	0.20	0.33	0.004
Copepoda	0.24	0.13	0.35	0.01
Nematoda	0.18	0.15	0.21	0.01
Diptera: Chironomidae	0.14	0.12	0.17	0.01
Plecoptera	0.08	0.08	0.08	0.01
Rotifera	0.02	0.02	0.03	0.0001
Diptera: Simuliidae	0.01	0.006	0.02	0.001
Microturbellaria	0.00	0.001	0.00	0.00001
Diptera: Tipulidae	0.001	0.001	0.001	0.0002
Collembola	0.0005	0.0005	0.0005	0.00003
Cladocera	0.0001	0.0001	0.0001	0.000004
Tardigrada	0.00005	0.00001	0.0001	0.000004
Ephemeroptera	0.00003	0.00003	0.00003	0.00001
Gastrotricha	0.00001	0.00001	0.00001	0.0000001
Trichoptera	0.00001	0.000006	0.00001	0.000001
Total	2.68	2.43	2.92	0.36

Lone Oak accounted for 84% of macrofaunal production, even although absolute values were much less (2.45 g m^{-2} yr^{-1}) than at Coweeta. At Lone Oak, however, meiofauna-sized oligochaetes (temporary meiofauna) were about 75% as productive as the macrofaunal insects as a whole. These data support the conclusions of Strayer and Likens (1986) and Poff et al. (1993), who also found that the meiofaunal size classes contribute significantly to community production, although Poff et al. (1993) found the permanent meiofauna to be most productive.

The large percentage contribution of the meiofauna to production at Lone Oak is of great potential interest. Oligochaetes, ostracods, copepods, and nematodes are clearly the most prominent, but even the meiofauna-sized insects in the Chironomidae and Plecoptera make a substantial contribution. The Chironomidae and some Plecoptera at Lone Oak are indeed mainly small bodied, including *Corynoneura, Stempellinella,* and *Eukiefferiella* among the chironomids and small leuctrids among the stoneflies. The distribution of biomass and density across the whole size range of body size in this study will form the subject of a subsequent paper, but our speculative reasons for the small size of many of the herbivore/detritivore species at Lone Oak include the stream's profound acidity and the prominence of predatory invertebrates in this fishless system.

Clearly, if this distribution of production among the size fractions was repeated in other streams, studies that do not include the meiofauna could substantially underestimate benthic community production. Failure to include the permanent meiofauna at Lone Oak would incur an underestimate of about 15%. Even quite large-bodied members of the permanent meiofauna (up to nearly 100 μg dry weight) were not retained on a 500-μm mesh. Based on this evidence, failure to represent the very small oligochaetes, ostracods, copepods, and nematodes, in particular, but also insects ($<$10 μg dry body weight) might increase the underestimation to more than 50%. However, we would stress that errors of this magnitude are unlikely in modern studies of production of benthic insects and macrocrustacea using net meshes of around 250 μm (e.g., Lugthart and Wallace 1992; Huryn 1996), in which much of the temporary meiofauna was probably accounted for.

On the other hand, Lone Oak may be somewhat unusual in terms of its low pH and fishless community. An intriguing question is whether these biotic and abiotic factors lead to an unusual disparity, compared with other streams, between the permanent meiofauna and macrofauna: for instance, if the microcrustacea were particularly scarce in acid streams (and some evidence supports this: Rundle and Hildrew 1990), meiofaunal production could be relatively still greater in circumneutral systems. Further, sampling only the top 5 cm of sediment, as in this study, ignores numerous interstitial invertebrates, which could add further to total secondary production (Smock et al. 1992; Stead et al. 2004). Evidence from this study suggests, therefore, that the meiofauna could be a significant component of overall productivity in the benthos. Meiofaunal production might be added, therefore, to the budget of Huryn (1996) to explain the apparent shortfall in the production of benthic invertebrates required to support trout in streams.

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