Secondary production of benthic communities at the habitat scale as a tool to assess ecological integrity in mountain streams

Andrea Buffagni & Ester Comin
Water Research Institute – C.N.R., Via della Mornera 25, I-20047 Brugherio (MI), Italy
E-mail: buffagni@server-mi.irsa.rm.cnr.it; ab1@mail.disat.unimib.it

Abstract

Secondary production of the benthic community was estimated in the four functional habitats identified in the pristine Pioverna stream (Northern Italy): riffle, pool, transition and bedrock habitats. The instantaneous growth, removal-summation and size-frequency methods were used to estimate production. Twelve taxa reached appreciable densities and presumably accounted for most of total benthic production. Three of them belong to the Plecoptera, seven to the Ephemeroptera and one each to Diptera and Trichoptera. The riffle habitat had the highest secondary production, while bedrock habitat had the lowest. Pool and transition habitats showed intermediate production values. Shredders and predators were the major component of production in pools, with a low contribution of gathering collectors. In riffles, this last category and scrapers had the highest production, with shredders, predators and filtering collectors showing decreasing production values. In general terms, shredders, gathering collectors and scrapers contributed most to total production. The rank-production curves for the habitats are reported. In riffles, a proportionally high evenness of the most productive taxa was noted. In contrast, in the pool habitat a steep curve was recognised. The potential of comparing rank/production curves and changes in reference species production between unaltered and impacted stream habitats and sites is discussed as a means to estimate ecological integrity. For site comparisons of secondary production in the alpine area, the riffle habitat is suggested as the most adequate, as it shows a lower dominance and more taxa contributing to overall production. The calculation of secondary production for indicator and dominant taxa in the different habitats should constitute an effective way to describe some functional aspects of the community to assess the ecological integrity of mountain streams.

Introduction

In general terms, ecological integrity can be intended as the sum of biological and physical elements and processes (Covich et al., 1998; Karr, 1993). Biological elements depend on biological and physical processes for their maintenance, and the degradation of ecological integrity results in global biotic impoverishment. Measures of ecological integrity – as regards biological attributes – should be based on population, community and ecosystem responses to disturbance (Covich et al., op. cit.); they often involve structural measures such as abundance, species richness and modifications of community composition. Functional measures are usually employed at the ecosystem level: e.g., energy flow, nutrient cycling,

primary and secondary production. Production is one of the major paths of energy flow through ecosystems (Waters, 1977), and even modest rates of secondary production could be linked to important organic matter processing and nutrient cycling within ecosystems (Fisher & Gray, 1983). In addition, it is a valuable response variable at population, community and ecosystem levels and the most comprehensive representation of success for any population (Benke, 1993). Furthermore, production estimates of invertebrate taxa are a powerful means to assess man-induced stress in aquatic environments in that they are a quantitative measure of ecosystem function (Benke, op. cit.); such estimates could be a key tool in defining ecological integrity. Nevertheless, to the authors' knowledge, few studies regarding benthic invertebrates have dealt

with the potential of production for measuring biological or ecological integrity, apart from the impact of organic pollution (e.g., Zelinka et al., 1977). Furthermore, very few of them were performed at the habitat scale (e.g., Smock et al., 1985). It has been argued (Harper et al., 1992) that conserving the river habitats themselves is a cost-effective surrogate for conserving the invertebrate community, and Harper et al. (1998a) demonstrated that the re-establishment of functional habitats is linked with geomorphological and ecological changes. Despite the widespread interest in the ecosystem processes, most of functional (and production) changes at the habitat scale due to river management practices and anthropogenic stress are still to be understood (e.g., Harper et al., 1998b).

The aim of this study is to highlight some aspects of secondary production estimates for aquatic invertebrates that could be used to assess ecological integrity in mountain rivers. Attention will be paid to the relative production of the most representative and abundant taxa, also according to trophic groups and different benthic habitats. In particular, we focus upon the use of the habitat scale in secondary production investigations.

Study site

The Pioverna is a typical mountain stream of the Italian Alps, located in Valsassina (Pasturo, Lecco, North Italy) with a drainage basin of 131.6 km^2. It flows between 418 and 2554 m a.s.l. and its waters run for about 20 km before running into the Como Lake, near Bellano. The collecting site is a pristine river stretch about 200 m long and 3 m wide at base flow, at 830 m a.s.l., close to the city of Pasturo. The minimum discharge was observed in April 1997 (0.011 m^{3}s^{-1}), the maximum in July 1997 (0.241 m^{3}s^{-1}), with an average discharge of 0.076 m^{3}s^{-1}.

The vegetation of the study site, which is only partially shaded, is typical of the southern slope of the Alps, with deciduous trees. *Alnus glutinosa*, *Quercus* spp., *Salix* spp., *Fraxinus excelsior*, *Corylus avellana*, *Acer pseudoplatanus* and *Robinia pseudoacacia* occur along the stream banks and in the steep adjacent areas. The sampling site had almost entirely stony or rocky substratum, with water velocity varying from 0 to about 2 ms^{-1}; maximum water depth was about 1 m. No aquatic macrophytes are present. Water temperature ranged from 3.5°C in December to 15.6°C in August, with an annual average of 7.8°C. The Pi-

overna stream is characterised by high calcium and magnesium bicarbonate concentration and exhibited average annual conductivity and pH of 469 mS/cm (at 20°C) and 7.7, respectively.

The studied reach showed very good water quality. On the date of sampling, the biological quality was evaluated by means of the Extended Biotic Index (Woodiwiss, 1964) modified by Ghetti (1986) for use in Italian streams. The values assumed by this biotic index were found to be constantly over 10 (Quality Class I), indicating non-polluted water or an environment unaltered in any detectable way.

Materials and methods

Benthic samples: A total of 115 Surber samples (area, 0.15 m^2; mesh size, 0.45 mm) were collected monthly from April 1996 to September 1997. On average three replicates were taken for each of the different habitats sampled. In total, about 17 000 larvae (belonging to 63 different taxa) were collected, sorted out in the field and fixed in 80% ethanol. Subsequently the individuals were identified in the laboratory to the following taxonomic levels: species (Ephemeroptera, Hirudinea, Mollusca, Isopoda and Diptera Athericidae), genus (Plecoptera, Odonata and Gammaridae) and family (Diptera, Trichoptera, Coleoptera, Oligochaeta and Turbellaria).

For each sampling area, the following variables were measured: flow velocity, depth, pH and conductivity. Furthermore, substratum composition (estimated visually as percentage composition) and bed roughness were calculated. Moreover, discharge was determined and instantaneous, minimum and maximum water temperatures were recorded every 2 weeks.

Estimation of secondary production: Densities and standing stocks were estimated for the most abundant taxa present at the study site. To allow life cycle descriptions and production appraisal, we measured body length of the selected taxa from the anterior edge of labrum to the posterior edge of the last abdominal segment (Welton et al., 1982), to the nearest 0.25 mm under a microscope.

To estimate production (dry weight) we used three methods: removal–summation (Boysen-Jensen, 1919; Brooker & Morris, 1978; Waters, 1979), instantaneous growth (Allen, 1949; Ricker, 1946; Waters, 1966) and Hynes–Hamilton (Hynes, 1961; Hamilton, 1969). In the first method, the mortality between successive samples, taking into account the size of organisms

during the period of loss, is calculated in terms of weight or biomass. The sum of such observed mortalities over the entire life cycle is equivalent to the total production of the cohort (Waters & Crawford, 1973). If the species is univoltine, the cohort production is equal to annual production. In the instantaneous growth method, for a given interval of time, production is calculated as the product of the instantaneous rate of growth (*G*) and the mean standing crop in weight (*B*) during the time interval. The formula used is: $P = G \cdot B$ (Allen, 1949; Ricker, 1946). For a given period of time, *G* is calculated as the natural logarithm of the ratio of the mean weight at the end of the period to the mean weight at the beginning of the period and *B* is computed as the average of the standing crops at the beginning and end of the period (Waters & Crawford, op. cit.). The Hynes's method differs from the others in that it divides a population into size classes rather than in sequential sampling periods. It is based upon the calculation of an 'average cohort', or the mean size distribution of animals collected over a year, and production is estimated as the sum of losses between successive size classes rather than between successive sampling dates (Waters, 1979). This method does not require the discrimination of single cohorts and can thus be used whenever the life cycle cannot be deciphered or when it is not possible to identify taxa to the species level. For the application of this method it is necessary to know the cohort production interval (CPI), that is the average period required for growth, from hatching to the attainment of maximum larval size (Georgian & Wallace,1983). For estimating the annual production of Hydropsychidae (Trichoptera) and *Protonemura* (Plecoptera), with no identifiable cohorts, we used this method only (asterisks in Figure 2). In all the other cases, the values resulted from averaging the production values obtained with the three methods. Taxa were assigned to functional feeding groups according to Ghetti (1986). The nymphs of the *Baetis alpinus* group (i.e., *B. alpinus* and *B. melanonyx*) were attributed to the scrapers category.

Production of benthic invertebrates was estimated in functional habitats (habitats with a real ecological meaning: Harper et al., 1992) previously identified in the Pioverna stream (Crosa & Buffagni, 1996) by means of the TWINSPAN analysis. These were defined by the composition and abundance of the benthic community. 'Riffle', 'pool', 'transition' and 'bedrock' habitat types were identified. The four habitats differ from each other mainly with regard to water velocity (pool and transition vs. riffle and bedrock),

depth (pool vs. the other habitats) and substratum features: granulometry (bedrock vs. the others) and substratum roughness (pool and bedrock vs. transition and riffle). The term 'transition' was used to label one habitat because it shows somewhat intermediate attributes between pools and riffles, not being properly identified with a 'run' habitat (Crosa & Buffagni, op. cit.). The transition habitat is highly dynamic, as it often occurs in stream areas where hydraulic features are expected to change even after a small discharge variation (e.g., lateral runs and marginal, still water, areas).

Results

In Figure 1, the percentage of occurrence of the collected taxa is reported – at the family or order level – for the four functional habitats. The abundance of a group of 12 taxa reached appreciable values (from 50% of total invertebrates in pools to 79% in bedrock habitats) and presumably accounted for most of total benthic production. Three of these taxa belong to the Plecoptera (*Amphinemura*, *Protonemura* and *Leuctra*), seven to the Ephemeroptera (*Alainites muticus* (Linné), *Baetis alpinus* (Pictet), *B. melanonyx* (Pictet), *B. rhodani* (Pictet), *Ecdyonurus helveticus* Eaton, *Rhithrogena* spp, *Habroleptoides auberti* (Biancheri)), and one each to Diptera (*Ibisia marginata* (Fabricius)) and Trichoptera (Hydropsychidae). Other taxa showed a relatively high density in particular habitats only. For example, the Chironomidae were common in pools and bedrock, the Helodidae in riffle and transition habitats, the Hydracarina in pools and the Oligochaeta in transition areas. These taxa were not included in the secondary production estimate since, for calculating their production, methodological difficulties could emerge, leading to unreliability of results. In many – and relevant – cases, the taxa's percentage of production was quite different from the equivalent percentage of numbers. For example, the Athericidae showed production percentages of 31 and 47 – in transition habitats and pools, respectively – against abundance percentages of 22 and 37. The Heptageniidae displayed, in riffles, 27% of production versus 17% of numbers and, in the transition habitat, 3 versus 20%. In this latter habitat, the Nemouridae contributed 33% to total production, while having only 16% of the individuals. In contrast, in the same habitat, the Leuctridae exhibited 4 vs. 8%, and, in pools, 23% of production against 40% of individuals.
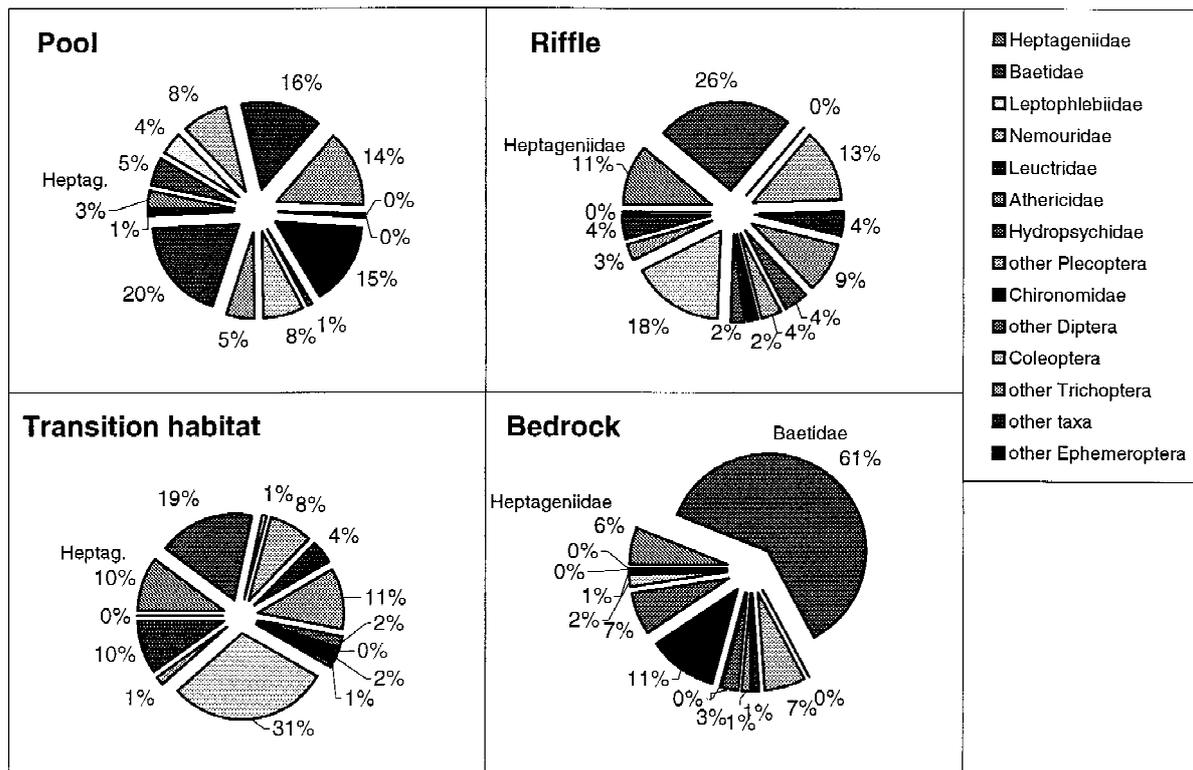
Figure 1. Relative abundance of the different families or orders of macroinvertebrates in each of the four Pioverna stream: pool, riffle, transition and bedrock. Families are reported clockwise from Heptageniidae to 'other Ephemeroptera', following the taxa list.

As regards the life cycle traits necessary to properly estimate production with removal–summation and instantaneous growth methods, the studied taxa showed different numbers of cohorts in one year. While *H. auberti* developed in one synchronous winter generation, all the other taxa exhibited two or three cohorts in 1 year. *E. helveticus*, *R. semicolorata*, *B. rhodani*, *B. alpinus*, *Leuctra* and *Amphinemura* presented three cohorts which could be followed (being bivoltine or multivoltine). These taxa and *I. marginata* were present year-round, while the remaining ones were found seasonally with two cohorts. A detailed presentation of the life cycle and production values of each taxon is beyond the aims of the present paper and will be the subject of a specific study (Buffagni, in prep.). The three methods used to estimate secondary production displayed high correlations. The Spearman's rho correlation coefficient was over 0.7 between each pair of methods and for any group of taxa. High correlations were present for the mayflies and *I. marginata* – identified at the species level – as well as for *Amphinemura* and *Leucra*,

especially between the Hynes–Hamilton and removal–summation methods. For these two latter taxa and methods, rho reached the highest value (0.931). This suggests that the non-specific identification – which could lead to inaccuracy in life cycle interpretation and production calculation for the stoneflies – did not obviously affect the production estimates.

The 'riffle' habitat had the highest secondary production, while 'bedrock' habitat had the lowest (Figure 2a). Pool and transition habitats showed intermediate production values. The total production of the community – for riffle, pool and transition habitats, respectively – was about 1.85, 0.66 and 0.65 g m^{-2} year^{-1}. Baetid and heptageniid mayflies, along with the dipteran Athericidae and plecopteran Nemouridae, made the greatest contribution to total production (Figure 2b–d). In the bedrock habitat, production was high only for the two mayflies *B. melanonyx* and *B. alpinus* (a total of 0.23 g m^{-2} year^{-1}). *I. marginata* exhibited a relatively high production in the three remaining habitats, while the other taxa showed more variability between habitats. For example, the heptageniid pro-

duction was quite high in the riffle habitat, but close to zero in the other ones. Secondary consumers should be kept separate from primary consumers; in the analysis of habitat production, however, they were considered together, as the only obvious predators are the Athericidae which are consequently easily distinguishable from the bulk of detritivores and herbivores.

Figure 3 a–c reports the rank–production curves for the three habitats pool, riffle and transition. A larger number of taxa (11) contributed to most of the riffle production than to pool production (five), with the transition habitat (eight) being intermediate. In the pool habitat a steep curve is recognisable, with *I. marginata*, *Amphinemura* and *Leuctra* giving the highest productions. In the riffle habitat two *Baetis* species, two Heptageniidae taxa, *Protonemura* and *I. marginata* had production values between 0.2 and 0.3 g m^{-2} year^{-1} (left side of Figure 3b). The remaining taxa displayed lower production (less than 0.1). In the transition habitat, three taxa (*I. marginata*, *Amphinemura* and *B. rhodani*) had a similar production of about 0.18 while all the other taxa had values less than 0.03 g m^{-2} year^{-1}. The rank–production curve for the site is reported in Figure 3d. The overall secondary production is here calculated on the basis of the integrated samples from all habitats, assuming that they were present with equal proportions. The resulting curve is, to some extent, similar to the riffle one, even if more uniform. In contrast, the rank ordination of the taxa is different. For example, *B. alpinus* shows at the site scale a much lower production and higher rank than in the riffle habitat, and the other riffle reference taxa change here their relative position along the production gradient.

Figure 4 shows the production values of the four habitats by macroinvertebrate feeding groups. Shredders and predators were the major component of production in pools, with a low contribution by gathering collectors. Anyway, since the Chironomidae production was not calculated, maybe the overall value for gathering collectors in this functional habitat is somewhat underestimated. In riffles, this latter category and scrapers had the highest production, with shredders, predators and filtering collectors showing decreasing production values. In transition habitats, shredders, predators and gathering collectors accounted for the highest proportions of benthic production, while filtering collectors and scrapers, even if present, made only a modest contribution. In general terms, shredders, gathering collectors and scrapers made the greatest contributions to total production. Scrapers and pred-

ator production proportions gradually increased and decreased, respectively, along an approximate velocity gradient (i.e. from pool to bedrock habitat).

Discussion and conclusion

Macroinvertebrate assemblages exhibited distinct production patterns among habitat types. This confirms the results of previous studies concerning benthic community production with respect to habitat type (e.g., Smock et al., 1985). In the Pioverna stream, the riffle habitat had the highest secondary production and bedrock habitat had the lowest. Antithetically, Wohl et al. (1995), in the southern Appalachians, found that cobble–riffle habitat had the lowest invertebrate biomass and productivity while the bedrock outcrops had the highest. Nevertheless, the latter habitat was characterised by the presence of standing crops of moss – absent from the Pioverna bedrock habitat – which were a suitable substratum for gathering collectors and filterers and which can explain this seeming discrepancy. In fact, aquatic macrophytes can represent a good habitat for taxa-rich and abundant macroinvertebrate communities (e.g., Gregg & Rose, 1985). For example, Grubaugh et al. (1997), estimating production in cobble and pebble/gravel habitats with and without macrophytes, noted that large standing crops of aquatic plant supported much greater production than plant-free areas. Comparing invertebrate communities of pool and riffles in North American low order rivers, Brown & Brussock (1991) found that riffle habitats contained more numbers, biomass and faunal richness than pools. The same occurred in the Pioverna stream (Buffagni, unpublished data) and corresponds to lower secondary production in pools than in riffles. In this respect, Brown & Brussock (1991) concluded that pool-adapted taxa are more likely to occur in different types of rivers where suitable refugia are available within the pool habitat substratum and flow reversals are less frequent. Hence, the observed lower production in the pool habitat of the Pioverna stream can be linked also to the unstable substrata in these areas, which are susceptible to scouting during spates (Grubaugh et al., 1997). Brown & Brussock (1991) also found – in agreement with the pattern observed in the Pioverna stream – that areas with intermittent flow (i.e., similar to the transition habitat) had lower densities and diversity than permanently submerged habitats (i.e., riffle habitat). The overall production estimated for the Pioverna stream is quite
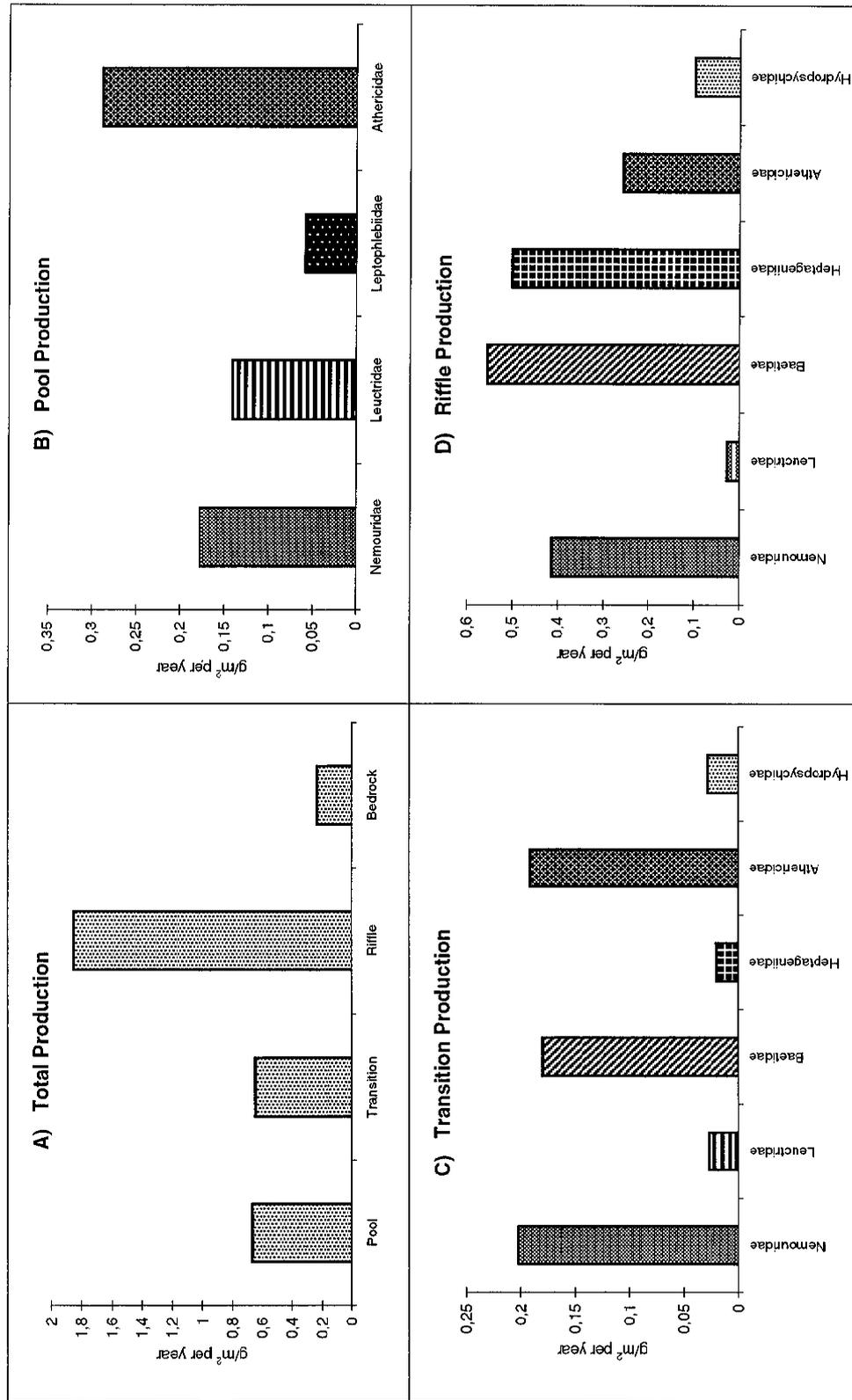
Figure 2. Production values of the whole community in the four functional habitats of the Pioverna stream (A) and of the different families of macroinvertebrates in each of the three more productive habitats: pool (B), transition (C) and riffle (D).
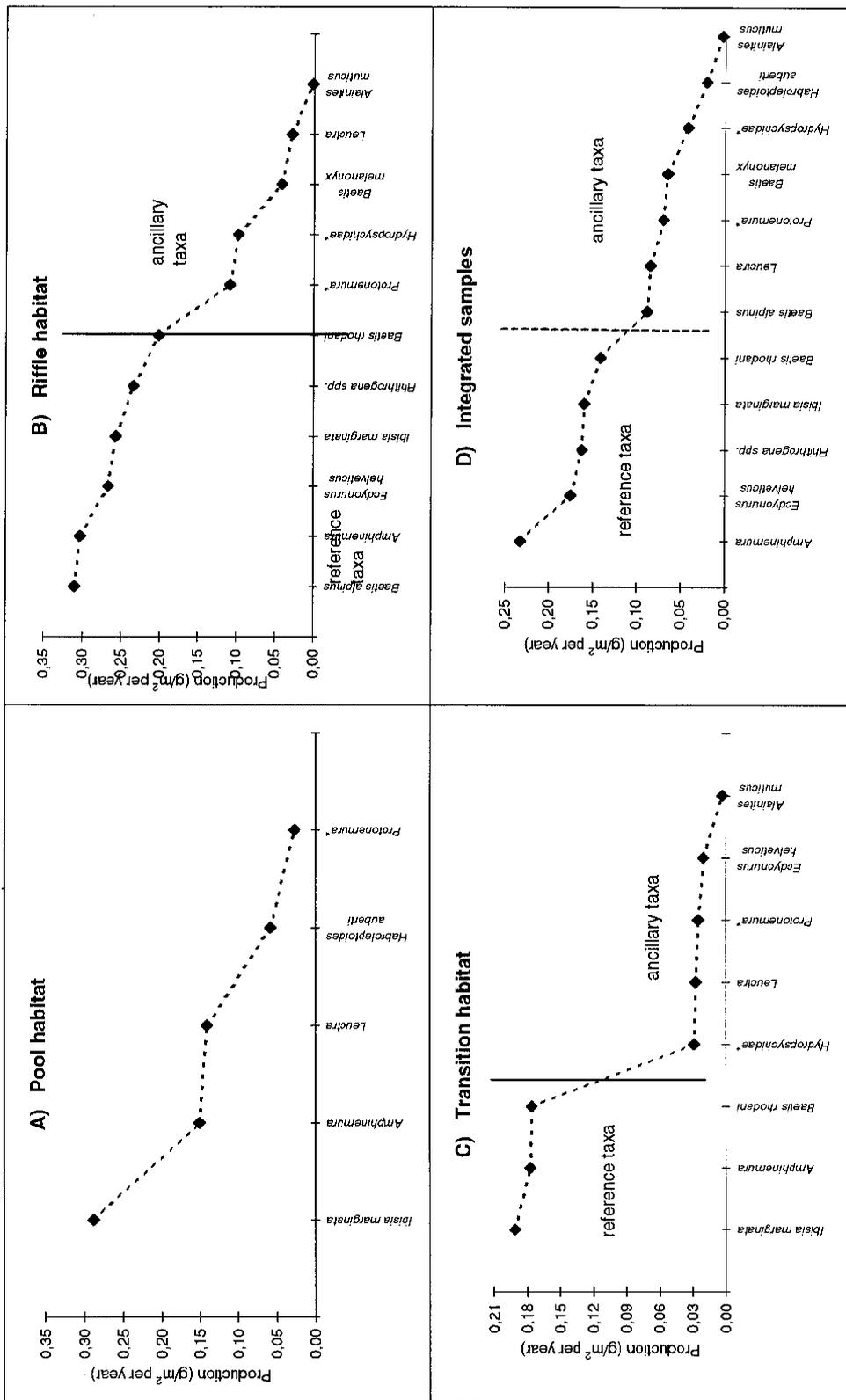
Figure 3. Rank–production curves for the three most productive functional habitats in the Pioverna stream, pool (A), riffle (B) and transition habitat (C), and the same from integrated samples from all the habitats.
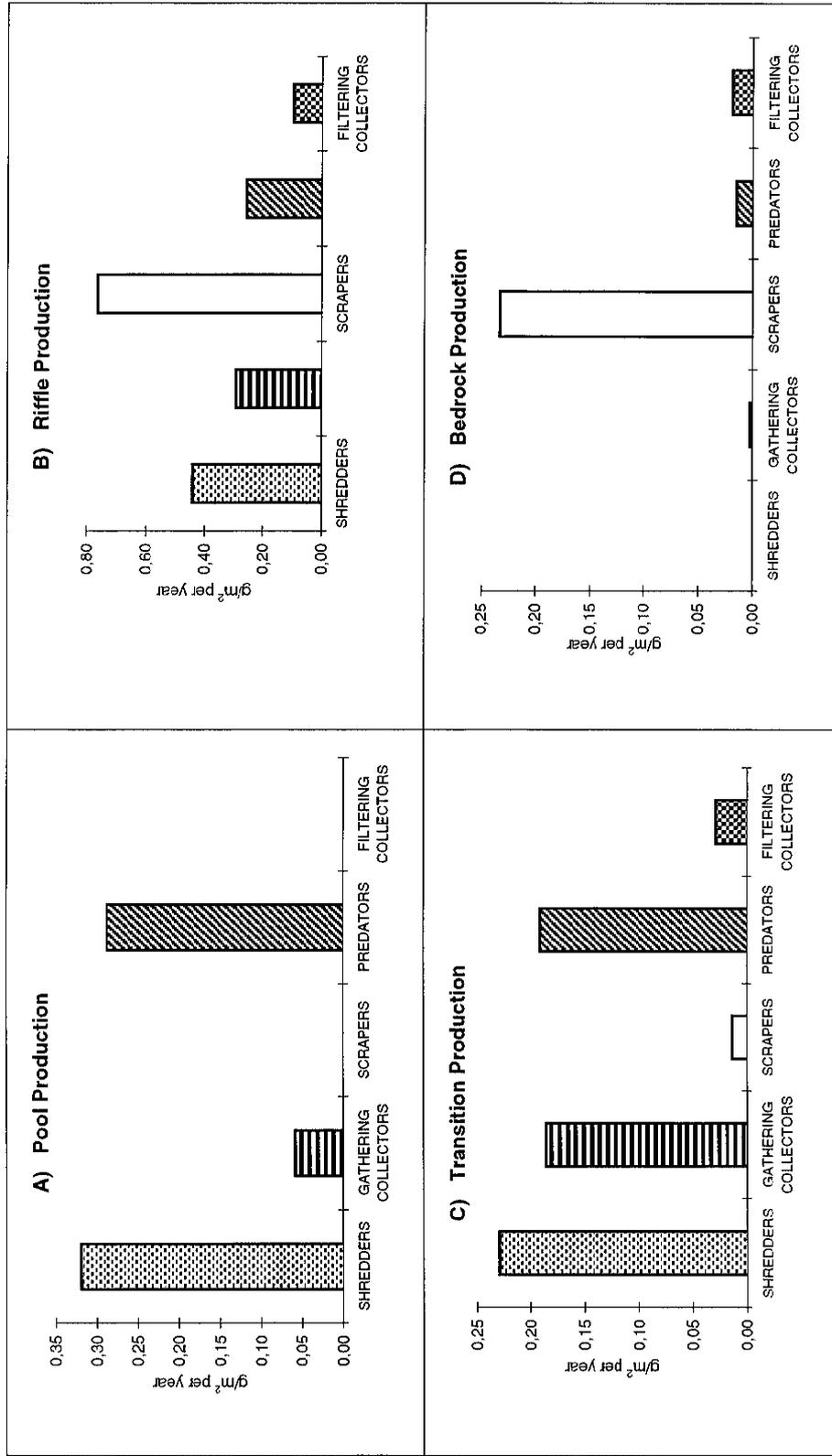
Figure 4. Production values by feeding groups of macroinvertebrates in the four functional habitats of the Pioverna stream: pool (A), riffle (B), transition (C) and bedrock (D) habitat.

low compared to values usually reported for rivers, and this is due to low densities of macroinvertebrates. Explanations can be sought in the frequent spates – and the presumably limited deposition of organic allochthonous detritus – which occurred during the rainy 1996 in the Pioverna stream, and in the paucity of the hyporheic component to the rocky sampling area: both probably affected overall densities (Dole-Olivier et al., 1997). Moreover, the study site is located in a narrow valley with little light and therefore low primary productivity.

According to Cao et al. (1997), it is desirable to split community variation in different forms to better assess man-induced impacts. In the same way, it could be worthwhile to split up the production data of the benthic community. Cao et al. (op. cit.) listed various types of change in species abundance as a result of organic pollution, assigning species as gained, lost or persisting. In the riffle habitat of the pristine Pioverna stream, about 10 taxa contributed with higher production values. A portion of these organisms are expected to modify their production in altered environmental conditions due to human activities (Frutiger, 1985). The production of some of those species will increase while that of others will decrease in the case of pollution, because of different sensitivity and response to stress. Taxa like the Hydropsychidae, *B. rhodani* and to a lesser extent *B. alpinus* would probably had increased production in many cases (e.g., Alba Tercedor et al., 1991; Janeva, 1979; Mackay & Waters, 1986; Zelinka et al., 1977), while the production of Heptageniidae *E. helveticus* and *Rhithrogena* and the Athericidae *I. marginata* would decrease (e.g., Bauernfeind et al., 1995; Leps et al., 1989; Malmqvist, 1996; Rivosecchi, 1984).

The rank–production curve in the riffle habitat reveals a proportionally high evenness (i.e., the relative taxa production is similar) of the most productive taxa ('reference' taxa: *B. alpinus*, *Amphinemura*, etc.; highest portion of the curve) and a quite evident separation from the less productive taxa ('ancillary' taxa: *Protonemura*, Hydropsychidae, etc.; lowest portion of the curve). Note that production of *Protonemura* and Hydropsychidae was estimated with the size–frequency method only, which usually gives higher values than the other methods used here (e.g., Iversen & Dall, 1989; Waters & Crawford, 1973). If studying production in impacted watercourses of the Pioverna stream type, once the species association has been defined, it would therefore be possible to evaluate which taxa, following environmental alteration, move

from the dominant to the ancillary category or vice versa, disappear or – for a new taxon – enter the major contributors to the macroinvertebrate production.

Comparing curves from different habitats of the Pioverna stream, it is notable that in the transition habitat (often characterised by unstable flow conditions, low primary productivity and by sharing most species with the riffle habitat (Buffagni & Crosa, unpublished)), three out of six riffle reference taxa show high production; these are *I. marginata*, *B. rhodani* and *Amphinemura*, which can be considered habitat generalists. *I. marginata* also lives within the substratum and is less affected by flow variations. In this case, dissimilarities between the two habitats are presumably due to the naturally differing physical features (e.g., lower water velocity in the transition habitat), although analogous changes in the list of reference species after habitat degradation or water pollution events are expected. In the event of a temporal shift from riffle to transition habitat due to environmental alteration (e.g., flow regulation), three taxa would drop out of the reference category and none would move in from the ancillary category. Furthermore, *Rhithrogena* and *B. melanonyx* would no longer be found in the community.

Examining the rank/production curve and comparing its shape between unaltered stream areas (i.e., with high ecological integrity) and impacted areas should demonstrate notable changes (e.g., Odum, 1988). In a curve closer to the broken-stick model (Wittaker, 1965), as seen in the riffle habitat of the Pioverna stream, the taxa's production trend would change, moving to higher dominance curves (i.e., typical of logarithmic and geometric series). In fact, a benthic community dominated by one or few taxa is often indicative of environmental stress (Plafkin et al., 1989) or low water resource quality (Kerans & Karr, 1994). The dominance of the community can be approximated by the percent contribution of the most productive taxon (Grubaugh & Wallace, 1995) and, where reference communities do exist, indices of community similarity can measure the loss of benthic species as well as changes in taxonomic composition, taxon abundance and production (Plafkin et al., op. cit.). Some indices enable more emphasis to be placed on selected species; they could perhaps be advantageously applied to production data as presented here, e.g., the Pinkham and Pearson Community Similarity Index (Pinkham & Pearson, 1976), as already recommended in biomonitoring protocols (Plafkin et al., op. cit.).

Zelinka et al. (1977) estimated macroinvertebrate production, at the site scale, in three stations along the Bítyska brook, a trout stream in the Czech Republic, characterised by different levels of saprobity: oligosaprobity (reference site), betamesosaprobity and polysaprobity. The unpolluted site showed the lowest dominance (and highest number of reference taxa) and the most strongly impacted one shows high dominance and very few species being productive. The moderately polluted station supported a community with intermediate production attributes (Zelinka et al., op. cit.). Grubaugh & Wallace (1995) estimated production at one site in the southeastern US before and after biotic integrity improved (after a 35-year period), reporting a shift in the dominant taxon from simuliids to hydropsychids. The same authors stated that this shift in dominance indicated an improvement in biotic integrity of the stream (Grubaugh & Wallace, op. cit.). At the site scale, evident gradients of river integrity therefore effect trends in community production relationships and dynamics. Examining the curve of secondary production estimated in the present paper from the integrated samples from all the habitats reveals a similarity with the riffle curve. As the riffle contributed most to total production, it is logical that the shape of the integrated sample curve resembles the riffle one. The rank-production curve from the integrated sample seems a rough surrogate, being reshaped by the production of taxa present in pool, transition and bedrock habitats. The derived, overall picture fails in describing a single habitat (i.e., riffle) reference situation and shows a taxa sequence that is not representative of any habitat, furthermore smoothing down inter-taxa production differences that are apparent within the single habitats. The community structure assessed – merging all the samples – therefore probably describes a situation of unsatisfactory ecological meaning, combining four distinct macroinvertebrate assemblages. The approach of studying secondary production by splitting up river stretches into the major macroinvertebrate functional habitats has been present in the literature for many years (e.g., Benke et al., 1984). In this regard, Smock et al. (1985) argued that it is important to adjust production according to habitat abundance in order to properly examine total stream productivity; this was confirmed by Lugthart & Wallace (1992), who measured the overall production weighting the proportional availability of the habitats. To estimate the production of a river stretch, a preliminary listing of the instream habitats is therefore required to obtain a representative sample, whether taking into account the habitats in equal proportion or according to their relative availability. Furthermore, an environmental impact could act on specific habitat types or on functional habitat occurrence (e.g., Kemp et al., 1999); this may lead to failure when assessing ecological impact using production estimates performed at the site scale. Besides, the occurrence and frequency of instream habitats reflects the main geomorphological processes in the river channel, allowing further assessment of anthropomorphic impact (Harper et al., 1998). Thus, calculating production at the functional habitat scale, rather than solely at the site scale, could represent a thorough and attainable approach to ecological integrity investigations. In addition, the identification and study of distinct aquatic habitats has an intuitive value, since habitats link the impacts on the natural environment and its inhabitants (Harper et al., 1995). Habitats also have a notable potential in river management because they can be easily recognised, whereas most taxa and ecological functions cannot (Harper et al., op. cit.). Harper et al. (1992) emphasised that within the set of habitats in which a taxon can potentially be present there is a smaller set which must be represented for the taxon to succeed. Assessing production at the habitat scale allows to list which habitat offers the best conditions for a particular species to develop; this has direct relevance in biodiversity conservation strategies to production estimates.

When trying to estimate river integrity (other than comparing absolute production values, which – in Alpine streams – can greatly vary among different years due to natural fluctuations), intertaxon and interhabitat relationships could be juxtaposed between reference and impacted sites. Furthermore, in habitats where a few species usually exploit the food resource – in polluted as well as in unaltered sites – production can attain high values (Grubaugh et al., 1997), without any clear link with ecological integrity. For site comparisons of secondary production in the Alpine area, the riffle habitat therefore seems to be the most adequate, as is implicitly assumed in other areas (Krueger & Waters, 1983), because it shows a lower dominance and more taxa contributing to overall production.

As the collected benthic invertebrates were represented by more than one trophic level, analysis can be done separating taxa according to their trophic role (Lugthart & Wallace, 1992). No studies have been conducted in Italian streams regarding the feeding habits and food types selected by invertebrates, and explicit investigations (i.e., gut analysis) should

be carried out to allow a truly representative attribution to functional feeding groups. For instance, some of the most productive taxa found in the Pioverna stream, such as the Heptageniidae (i.e., *Ecdyonurus helveticus* and *Rhithrogena*), seem to be able to feed both on scrapers and gatherers, depending on habitat type, food availability and nymphal size (e.g., McShafferty & McCafferty, 1986); the *Baetis* species can easily vary their feeding group too. Notwithstanding these uncertainties on group attribution, in the study of the relative importance of trophic roles, production as a functional measure of ecological integrity seems potentially informative (Benke, 1993). According to longitudinal trend predictions of the River Continuum Concept (Vannote et al., 1980) and to previous studies (Grubaugh et al., 1997), the shredders', gathering collectors' (and here scrapers') contribution to production were the greatest in the low-order Pioverna stream. Similarly to previous works (Grubaugh & Wallace, 1995 for *Baetis* spp.), the *Baetis* species of the *alpinus* group – dominant in the bedrock and riffle habitats – were classified into the scrapers category, leading to a high production percentage of this feeding group. Very small quantities of fine organic material, compared with aufwuchs, were available in the bedrock habitat, supporting this attribution. As far as the proportions of production in the four sampled habitats are concerned, notable differences were recorded among feeding groups. While shredder organisms were a major and filtering collectors a minor component in all of them, gathering collectors, scrapers and predators showed a clear variability among habitats. The relative contributions to annual production by functional groups mostly confirm results from other studies (e.g., Wohl et al., 1995); major differences concern the low contributions of gathering collectors in pools and filter-feeders in bedrock habitats. The absence of the Chironomidae production percentage, not calculated here, from the gathering collectors group can in part explain this discrepancy in pools. In general terms, the proportion of scrapers and predators within single habitats seems suitable to be used as an indicator of biotic integrity in Alpine streams, as stated for other geographic areas (Kerans & Karr, 1994). Apart from classifying taxa into specific functional feeding groups, in order to measure the integrity of the benthic community and habitat quality, Frutiger (1985) suggested using the ratio between production by primary and secondary consumers. This ratio is expected not to exceed 15 in undisturbed Alpine rivers – in the Pioverna stream it was below 8 – and to increase in impacted sites (Frutiger, op. cit.). The application of equivalent ratios at the habitat scale seems promising since it could limit estimation inaccuracy induced by inter-habitat variability of production. The *P/B* ratio, too, can be suitably used at the habitat scale to evaluate shifts of the invertebrate assemblages to smaller taxa with shorter generation time (Lugthart & Wallace, 1992) or to assess the habitat-specific variation of population structure for single indicator taxa after disturbance.

Production studies therefore seem to represent an important tool for examining the effect of disturbance in lotic ecosystems (Benke, 1984). Lugthart & Wallace (1992) demonstrated that production estimates can better assess the impact of disturbance than abundance and biomass, two critera more frequently employed in river integrity evaluations. These authors (Lugthart & Wallace, op. cit.) proved that, in mountain Appalachian streams, measures of abundance did not reflect the importance of shredders and predators, while biomass calculation underestimated the role of small-sized gathering collectors. In general terms, abundance and biomass measures tend to under- or overestimate the roles of taxa in river ecosystems (e.g., Benke et al., 1984; Wohl et al., 1995). Production is potentially a very useful measure as it combines effects on population and community function; it therefore synthesises information about a variety of perturbations. Even if not adequate for rapid and 'one-sample' bioassessment, secondary production estimates can be an effective tool for more detailed studies. These would include regularly monitored river systems or areas of declared social or naturalistic interest. Moreover, they could be fruitfully carried out in long-term programs aimed at identifying changes in ecosystem processes on a basin-wide scale. In addition, in many cases, the product of the mean biomass and the annual *P/B* ratio of each taxon could be used to estimate the annual production (Lapachin & Neveu, 1980; Mortensen & Simonsen, 1983; Waters, 1977). This would reduce time, depress costs and simplify estimates, giving secondary production higher monitoring effectiveness.

As confirmed by the present research, benthic secondary production may vary greatly between the different in-channel habitats (Smock et al., 1985). For this reason, calculating an overall mean value for secondary production could be inadequate to evaluate specific functional aspects of ecosystem integrity. Instead, secondary production should be estimated for each of the most important constituent habitats. In the

194

present study, calculating secondary production for dominant and indicator taxa in the different habitats was an effective way to describe reference conditions against which the ecological integrity of mountain streams can be measured.

Acknowledgements

References

Alba Tercedor, J., C. Zamora Munoz, A. Sàncez Ortega & I. Guisasola, 1991. Mayflies and stoneflies from the Rio Monachil (Sierra Nevada, Spain) (Ephemeroptera and Plecoptera). In: Alba Tercedor, J. & J. Sanchez Ortega (eds), Overview and Strategies of Ephemeroptera and Plecoptera Sandhill-Crane Press: 529–538.

Allen, K. R., 1949. Some aspects of the production and cropping of fresh waters. Trans. r. Soc. N. Z. 77: 222–228.

Bauernfeind, E., P. Weichselbaumer & O. Moog, 1995. Ephemeroptera. In: Moog, O. (ed.), Fauna Aquatica Austriaca, Teil 3, Lief. 1/1995, BMLF., Wasserkataster, Wien: 1–17.

Benke, A. C., 1984. Secondary production of aquatic insects. In: Resh V. H. & D. M. Rosemberg (eds), Ecology of Aquatic Insects. Praeger Publishers, New York: 289–322.

Benke, A. C., 1993. Concepts and patterns of invertebrate production in running waters. Verh. int. Ver. Limnol. 25: 15–38.

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

Boysen-Jensen, P., 1919. Valuation of the Limfjord. 1. Rep. Dan. Biol. Sta. 26: 3–44.

Brooker, M. P. & D. L. Morris, 1978. Production of two species of Ephemeroptera (*Ephemerella ignita* Poda and *Rhithrogena semicolorata* Curtis) in the upper reaches of the R. Wye, Wales. Verh. int. Ver. Limnol. 20: 2600–2604.

Brown, A. V. & P. P. Brussock, 1991. Comparison of benthic invertebrates between riffles and pools. Hydrobiologia 220: 99–108.

Cao, Y., A. W. Bark & W. P. Williams, 1997. Analysing benthic macroinvertebrate community changes along a pollution gradient: a framework for the development of biotic indices. Wat. Res. 31: 884–892.

Covich, A. P., W. H. Clements, K. D. Fausch, J. D. Stednick, J. Wilkins-Wells & S. R. Abt, 1998. Ecological integrity and western water management: a Colorado perspective. Department of the Interior, US Geological Survey. Colorado Water Resources Research Institute: Grant Number 14-08-0001-G2008/3, project 12.

Crosa, G. & A. Buffagni, 1996. L'habitat idraulico quale elemento per la gestione degli ambienti fluviali. S.It.E. Atti. 17: 581–583.

Dole-Olivier, M. J., P. Marmonier & J. L. Beffy, 1997. Response of invertebrates to lotic disturbance: is the hyporheic zone a patchy refugium? Freshwat. Biol. 37: 257–276.

Fisher, S. G. & L. J. Gray, 1983. Secondary production and organic matter processing by collector macroinvertebrates in a desert stream. Ecology 64: 1217–1224.

Frutiger, G., 1985. The Production Quotient PQ: a new approach for quality determination of slightly to moderately polluted running waters. Arch. Hydrobiol. 104: 513–526.

Ghetti, P. F., 1986. I macroinvertebrati nell'analisi di qualità dei corsi d'acqua. Provincia autonoma di Trento, Trento, 105 pp.

Georgian, T. & J. B. Wallace, 1983. Seasonal production dynamics in a guild of periphyton-grazing insects in a Southern Appalachian stream. Ecology 64: 1236–1248.

Gregg, W.W. & F. L. Rose, 1985. Influences of aquatic macrophytes on invertebrate community structure, guild structure, and microdistribution in streams. Hydrobiologia 128: 45–56.

Grubaugh, J. W. & J. B. Wallace, 1995. Functional structure and production of the benthic community in a Piedmont river: 1956–1957 and 1991–1992. Limnol. Oceanogr. 40: 490–501.

Grubaugh, J. W., J. B. Wallace & E. S. Houston, 1997. Production of benthic macroinvertebrate communities along a southern Appalachian river continuum. Freshwat. Biol. 37: 581–596.

Hamilton, A. L., 1969. On estimating annual production. Limnol. Oceanogr. 14: 771–782.

Harper, D. M., C. D. Smith & P. J. Barham, 1992. Habitats as the building blocks for river conservation assessment. In: Boon, P. J., P. Calow & Petts G. E. (eds), River Conservation and Management. John Wiley, Chichester: 311–319.

Harper, D. M., C. D. Smith, P. J. Barham & R. Howell, 1995. The ecological basis for the management of the natural river environment. In: Harper, D. M. & Ferguson A. J. D. (eds), The Ecological Basis for River Management. John Wiley & Sons Ltd, Chichester: 219–238.

Harper, D. M., M. Ebrahimnezhad & F. Climent, 1998a. Artificial riffles in river rehabilitation: setting the goals and measuring the successes. Aquat. Conserv. Mar. Freshwat. Ecosyst. 8: 5–16.

Harper, D. M., C. D. Smith, J. L. Kemp & G. A. Crosa, 1998b. The use of 'functional habitats' in the conservation, management and rehabilitation of rivers. In: Bretschko, G. & J. Halesic (eds), Advances in River Bottom Ecology. Backhuys Publishers, Leiden, The Netherlands: 315–326.

Hynes, H. B. N., 1961. The invertebrate fauna of a Welsh mountain stream. Arch. Hydrobiol. 57: 344–388.

Iversen, T. M. & P. Dall, 1989. The effect of growth pattern, sampling interval and number of size classes on benthic invertebrate production estimated by the size-frequency method. Freshwat. Biol. 22: 323–331.

Janeva, I., 1979. Einige Vertreter der Gattung Baetis (Ephemeroptera) als Limnosaprobe Bioindicatoren. In Pasternak & Sowa (eds), Proceedings of the Second International Conference on Ephemeroptera, Krakow: 139–143.

Karr, J., 1993. Defining and assessing ecological integrity: beyond water quality. Envir. Toxicolo. Chem. 12: 1521–1531.

Kemp, J. L., D. M. Harper & G. A. Crosa, 1999. Use of 'functional habitats' to link ecology with morphology and hydrology in river rehabilitation. Aquat. Conserv. Mar. Freshwat. Ecosyst. 9: 159–178.

Kerans, B. L. & J. R. Karr, 1994. A benthic index of biotic integrity (B-IBI) for rivers of the Tennessee Valley. Ecolo. Appli. 4: 768–785.

Krueger, C. C. & T. F. Waters, 1983. Annual production of macroinvertebrates in three streams of different water quality. Ecology 64: 840–850.

Lapachin, L. & A. Neveu, 1980. The production of benthic invertebrates: comparison of different methods. Acta Ecolo. Ecol. Gener. 1: 307–322.

Leps, J., T. Soldàn & V. Landa, 1989. Multivariate analysis of compositional changes in communities of Ephemeroptera (Insecta) in the Labe basin, Czechoslovakia – A comparison of methods. Coenoses 4: 29–37.

Lugthart, G. J. & J. B. Wallace, 1992. Effects of disturbance on benthic functional structure and production in mountain streams. J. N. am. Benthol. Soc. 11: 138–164.

Mackay, R. J. & T. F. Waters, 1986. Effects of small impoundments on hydropsychid caddisfly production in Valley Creek, Minnesota. Ecology 67: 1680–1686.

Malmqvist, B., 1996. Bäckbromsen, *Atherix ibis* (Diptera: Athericidae), i Sverige: en rödlistad flugas utbredning och status. Ent. Tidskr. 117: 23–28.

McShafferty, D. & W. P. McCafferty, 1986. Feeding behaviour of Stenonema interpunctatum (Ephemeroptera: Heptageniidae). J. N. am. Benthol. Soc. 5: 200–210.

Mortensen, E. & J. L. Simonsen, 1983. Production estimates of the benthic invertebrate community in a small Danish stream. Hydrobiologia 102: 155–162.

Odum, E. P., 1988. Basi di ecologia. Piccin ed., Padova, 544 pp.

Pinkham, C. F. A. & J. B. Pearson, 1976. Applications of a new coefficient of similarity to pollution surveys. J. Wat. Pollut. Contr. Fed. 48: 717–723.

Plafkin, J. L., M. T. Barbour, K. D. Porter, S. K. Gross & R. M. Hughes, 1989. Rapid bioassessment protocols for use in streams and rivers: benthic macroinvertebrates and fish. EPA/444/4-89-001, Office of Water (WH-553), US Environmental Protection Agency.

Ricker, W. E., 1946. Production and utilization of fish populations. Ecol. Monogr. 16: 373–391.

Rivosecchi, L., 1984. Guide per il riconoscimento delle specie animali delle acque interne italiane. 28. Ditteri (Diptera). C.N.R., S. Ruffo (ed.), Verona, 177 pp.

Smock, L. A., E. Gilinsky & D. L. Stoneburner, 1985. Macroinvertebrate production in a southeastern United States stream. Ecology 66: 1491–1503.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell & C. E. Cushing, 1980. The river continuum concept. Can. J. Fish. aquat. Sci. 37: 130–137.

Waters, T. F., 1966. Production rate, population density and drift of a stream invertebrates. Ecology 47: 595–604.

Waters, T. F., 1977. Secondary production in inland waters. Adv. Ecol. res. 10: 91–164.

Waters, T. F., 1979. Influence of benthos life history upon the estimation of secondary production. J. Fish. Res. Bd Can. 336: 1425–1430.

Waters, T. F. & G.W. Crawford, 1973. Annual production of a stream mayfly population: a comparison of methods. Limnol. Oceanogr. 18: 286–296.

Welton, J. S., M. Ladle & J.A.B. Bass, 1982. Growth and production of five species of Ephemeroptera larvae from an experimental recirculating stream. Freshwat. Biol. 12:103–122.

Whittaker, R. H., 1965. Dominance and diversity in land plant communities. Science 147: 250–260.

Wohl, D. L., J. B. Wallace & J. L. Meyer, 1995. Benthic macroinvertebrate community structure, function and production with respect to habitat type, reach and drainage basin in the southern Appalachians (U.S.A.). Freshwat. Biol. 34: 447–464.

Woodiwiss, F. S., 1964. The biological system of stream classification used by the Trent River Board. Chem. Indust. 14: 443–447.

Zelinka, M. & Working Team, 1977. Production conditions of the polluted trout brook. Folia Fac. Sci. Nat. Univ. Purkynianae Brunensis XVIII, Biol. 60: 1–105.