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Benthic invertebrate production—facilitating answers to ecological riddles in freshwater ecosystems

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Abstract. Invertebrate secondary production, or the formation of invertebrate biomass through time, has been estimated in many freshwater benthic habitats. It has been a major research theme for the North American Benthological Society (NABS), and many of its members have made significant contributions to the subject, both before and during the existence of *J-NABS*. Although some benthic production work occurred before 1960, the major methods were developed primarily during the 1960s and 1970s. Most of these methods also were applied in terrestrial and marine environments. The main focus of our paper is how secondary production has been used as an essential variable in facilitating answers to a wide variety of ecological questions. Benthic freshwater production studies before the inception of *J-NABS* were primarily related to life history, interpopulation comparisons, niche overlap/competition, predator–prey relationships, differences in production/biomass (P/B), energy flow, the trophic basis of production, habitat-specific microdistributions, effects of pollution and dams, and quantification of aquatic–terrestrial linkages. Since that time, new applications have been related to habitat-specific macrodistributions, quantitative food webs, experimental and tracer-based studies of trophic resources, chemical flows/stoichiometric relationships, diversity/function relationships, influence of nonnative species and landuse changes, implications of metabolic theory, and the importance of meiofauna vs macrofauna. *J-NABS* has been a major outlet for many of these applications, has probably included a higher fraction of papers incorporating secondary production analysis than any other journal, and probably will continue to be a leader in this area.

Key words: macroinvertebrate, invertebrate secondary production, stream, lake, wetland, marine, benthic, terrestrial, ecological questions, predation, bioenergetics, energy flow.

Freshwater benthic studies have progressed over the last several decades from descriptions of life histories, distributions, and diversity to studies with increased emphasis on ecological processes, or *ecological function*, including energy flow, organic matter dynamics, primary and secondary production, and decomposition (**Benke et al. 1988**[3], **Tank et al. 2010**). The vast majority of secondary production studies have focused on invertebrates (for microbial production, see **Findlay 2010**) where an accurate and precise estimation of production is a crucial requirement for energy flow analysis. Invertebrate production, or their formation of biomass through time, has now been estimated for a wide range of freshwater habitats, especially streams and rivers (see reviews by Benke 1993, Huryn and Wallace 2000; Fig. 1). The rate of biomass turnover, often expressed as annual production divided by mean biomass (P/B), is a major component of production. P/B varies widely among populations and environments and is a calculation of considerable importance in itself (e.g., Benke and Huryn 2006; Fig. 1).

Secondary production had become a topic of interest for ecologists by the 1960s, and North American Benthological Society (NABS) members have been leaders in developing this area. Noel Hynes, the 1st NABS Award of Excellence winner, developed the most widely used method for freshwater benthos (Hynes and Coleman 1968; Fig. 1), now called the *size–frequency* method. Several papers by the 2nd NABS Award of Excellence winner, Tom Waters, inspired decades of benthologists to study secondary production (e.g., Waters and Crawford 1973, Waters 1977; Fig. 1). Although these contributions predated the first issue of the *Journal of the North American Benthological Society* (*J-NABS*), they clearly set the

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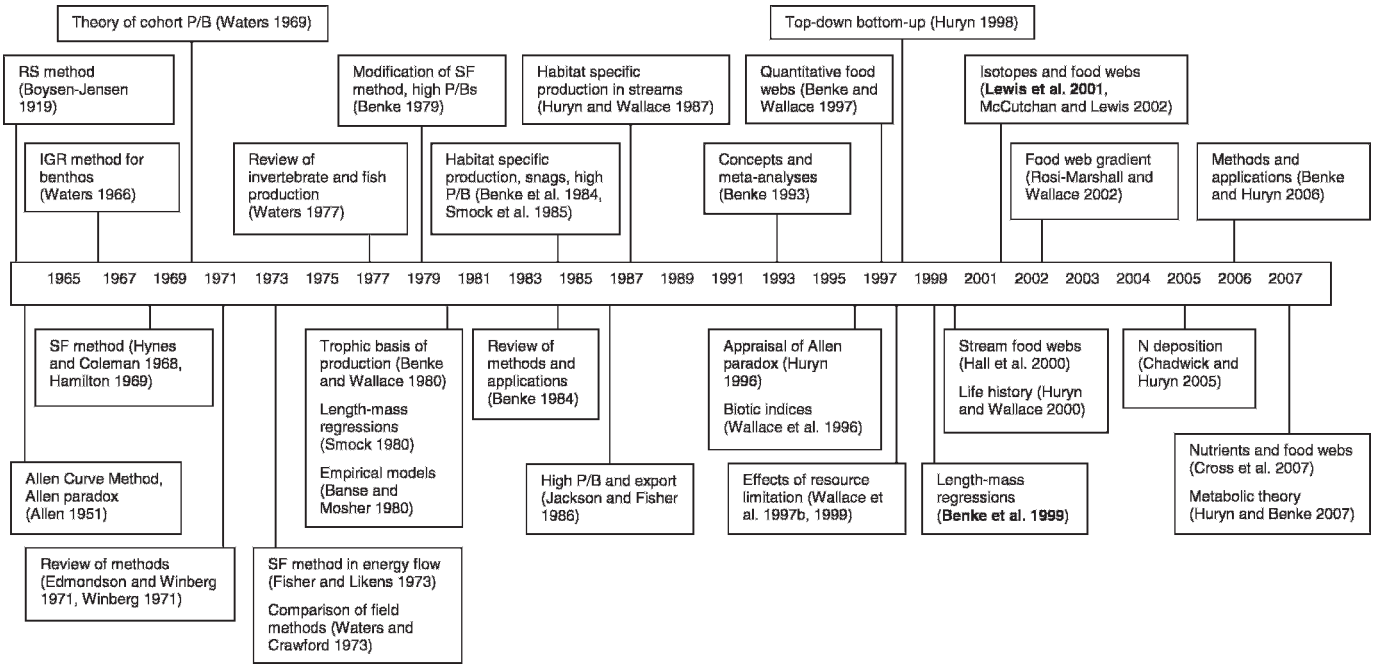


FIG. 1. Timeline of significant benthic invertebrate production studies from 1919 to present. RS = removal–summation method, IGR = instantaneous growth rate method, SF = size–frequency method, P/B = production/biomass. Boldface indicates paper was published in *J-NABS*.

stage for further study of secondary production, and resulted in numerous key papers. Approximately 6% of all papers in *J-NABS* have been on or have been related to benthic invertebrate production, undoubtedly a higher percentage than in any other journal.

We review advances in the study of freshwater benthic invertebrate production and how *J-NABS* has played a role in these developments. Our main focus is on identifying the many ways that secondary production has been used to facilitate answers to a variety of ecological questions. This paper is not intended to be a comprehensive review of secondary production, but we cite many papers relating to these questions.

History and Methods of Secondary Production

Aquatic ecologists have estimated production of zooplankton, benthic invertebrates, and fishes in marine, lake, and stream environments for many decades (Fig. 1). Work in inland waters has been well documented in various publications, especially through the mid-1970s by Waters (1977). The study of aquatic invertebrate production began with the application of the first cohort method to marine taxa by Boysen-Jensen (1919; Fig. 1), but the significance of this work was not realized for several decades. Other early aquatic production work was done in Russia (summarized by Winberg 1971; Fig. 1). The study of secondary production was greatly stimulated by the International Biological Program (IBP) of the 1960s, particularly by publication of IBP handbooks on freshwater fishes (Ricker 1968), freshwater invertebrates (Edmondson and Winberg 1971; Fig. 1), marine invertebrates (Holme and McIntyre 1971), and terrestrial animals (Petrusewicz and Macfadyen 1970). Most methods from these handbooks depended on following cohort survivorship and individual growth through time directly from field samples. Annual production could be calculated with the increment–summation method ($P=\sum \overline{N}\Delta W$) where $\overline{N}$ is population density and ΔW is the increase in mean individual mass between sampling intervals or with other cohort methods, such as the Allen curve, removal–summation, and field-based instantaneous growth methods, which are closely related variations of the increment–summation method (e.g., Gillespie and Benke 1979, Benke 1984 [Fig. 1]).

Studies of stream benthic production initially lagged behind those for marine and lentic freshwater habitats with only 4 direct estimates in streams through the 1960s (Hynes 1970, Waters 1977). Currently, however, production estimates for individual stream benthic populations are probably greater than all marine (benthic and planktonic), lake (benthic and planktonic), and fish production estimates combined. At least 3 reasons for this imbalance can be identified. An early impetus for work on stream benthos came

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from studies of salmonid production from the 1950s through the 1970s (Waters 1988). These studies, which had the goal of understanding factors underlying fishery production, also generated accurate estimates of benthic prey production, hence, the dual role of the early benthic production pioneers as fisheries, as well as benthic, ecologists (e.g., K. R. Allen, T. F. Waters). Several papers by Waters provided a particularly strong push towards stream benthic production work. These papers included his theoretical analysis of cohort P/B (Waters 1969; Fig. 1), his clear comparison of production methods using a stream mayfly (Waters and Crawford 1973), and his review of the freshwater production literature (Waters 1977). Last, development of the size–frequency method by Hynes and Coleman (1968) was a noncohort approach that allowed production calculations without the need to follow cohorts through time, and set the stage for an enormous number of production estimates. Although this method was initially controversial and required corrections (Hamilton 1969, Benke 1979; Fig. 1), its application made possible the inclusion of hundreds of population estimates in single publications (e.g., see Wallace et al. 1999; Fig. 1). More recent applications of these field-based methods to freshwater ecosystems are found in Benke (1984, 1993) and Benke and Huryn (2006).

Several shortcut approaches to estimating secondary production have been proposed over the years, but *empirical* models have received the most attention. With the accumulation of production estimates in the literature, some investigators have used regression analysis to examine the relationship between production, P/B, or growth rate and more easily measured variables, such as lifespan, temperature, or body size (Robertson 1979, Banse and Mosher 1980 [Fig. 1], Plante and Downing 1989, Morin and Bourassa 1992, Benke 1993, **Morin and Dumont 1994**). The resulting regressions have been called empirical models from which P/B, for example, can be estimated from body size, and multiplied by field-estimated biomass to obtain production. The appropriateness of model-derived production as a substitute for direct production methods has received considerable discussion (e.g., Benke 1993, **Morin and Dumont 1994**, **Morin 1997**). Nonetheless, this approach appears to be useful for large unwieldy systems such as the Orinoco River floodplain (**Lewis et al. 2001**; Fig. 1), broad-scale comparisons of multiple systems (e.g., Benke et al. 1998), and rare or very small species within an assemblage context (e.g., Strayer and Likens 1986, Benke and Wallace 1997 [Fig. 1]). Morin and collaborators have combined empirical models with other cost-saving approaches to make multisystem comparisons, an approach they suggest is appropriate for assessing anthropogenic impacts (**Morin and Dumont 1994**, **Morin et al.** 1995, **2004**, **Stephenson et al. 2007**).

An essential feature of any taxon-based assessment of production is the need for reliable estimates for size-specific mass. An efficient way to obtain individual mass is by conversion from length measurements using length–mass regressions. Smock (1980; Fig. 1) was the first to present equations for many North American aquatic insects that were an enormous help to others estimating production. Benke et al. (**1999**; Fig. 1) updated Smock's paper and added several hundred new equations (including noninsect invertebrates) for North America. Regressions also have been published for multiple taxa in other regions: Canada (Johnston and Cunjak 1999), Europe (Meyer 1989, Wenzel et al. 1990, Burgherr and Meyer 1997, González et al. 2002, Baumgärtner and Rothhaupt 2003), New Zealand (Towers et al. 1994, Stoffels et al. 2003), and Argentina (Miserendino 2001). Investigators studying production now have the choice of using published equations or developing their own.

Measurements of Secondary Production in Ecosystems other than Freshwater

Marine benthos

A brief comparison of invertebrate production from other environments, such as marine benthos and terrestrial ecosystems, can be instructive in highlighting the role played by freshwater benthologists and *J-NABS*. Studies in marine environments have paralleled those in freshwaters, as indicated by detailed treatments in 3 editions of IBP handbooks for marine benthos (Crisp 1971, 1984, van der Meer et al. 2005), and >200 publications over the last several decades (Cusson and Bourget 2005). Cohort methods and the size–frequency method are widely used in both marine and freshwater environments, particularly for single species or a few species studied simultaneously. In contrast, far fewer studies have been done of entire invertebrate assemblages from marine than from freshwater environments, possibly the result of sampling difficulties or a much greater diversity of life-history types and phyla in the marine environment. These same sampling difficulties and diversity differences are probably the major reasons for greater use of empirical models in marine studies (e.g., Robertson 1979, Banse and Mosher 1980, Brey 1990, Tumbiolo and Downing 1994). Production values for marine benthos (e.g., Cusson and Bourget 2005) appear somewhat similar to those for freshwater benthos (e.g., Benke 1993, Huryn and Wallace 2000). In a recent meta-

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analysis of 547 production data sets derived for benthic marine macroinvertebrates in 147 studies, Cusson and Bourget (2005) reported annual production from 0.2 mg dry mass (DM)/m^2 to 3.3 kg DM/m^2 (median = 1.8 g/m^2) per taxon, annual P/Bs from 0.004 to 36.7 (median = 1.96), and life spans from 0.2 to 50 y (median = 2 y). Furthermore, they found that production is strongly related to biomass, P/B is strongly related to life span and temperature, and the highest producers are often filter-feeders, all patterns commonly reported in streams.

Terrestrial ecosystems

Studies of terrestrial invertebrate production were also underway by the 1960s (Wiegert and Petersen 1983). Much of the terrestrial literature involved total bioenergetic analyses (including ingestion, assimilation, etc.; Petersen and Luxton 1982, Wiegert and Petersen 1983), but cohort methods also were used (see IBP handbook by Petrusewicz and Macfadyen 1970). Cohort methods were first applied to grasshoppers (Smalley 1960), which have continued to be a popular group for production studies over the decades (Wiegert 1965, Duke and Crossley 1975, Kaushal and Vats 1984, Meyer et al. 2002). The size–frequency method also has been applied to several terrestrial nonarthropod populations, including snails (Staikou et al. 1988, Staikou and Lazaridou-Dimitriadou 1990), earthworms (Whalen and Parmelee 2000), and nematodes (Doroszuk et al. 2007). However, in spite of several excellent terrestrial studies, application of production analysis is far rarer in terrestrial than in aquatic environments (Benke 2010), and we are unaware of any attempts to estimate production of entire invertebrate assemblages. Most terrestrial ecologists seem unaware of the potential of these methods for addressing many of the ecological questions described below. For example, Saint-Germain et al. (2007) recently emphasized the virtues of using biomass instead of densities in terrestrial arthropod community analyses, as a better surrogate for ''function'' than abundance (with no mention of production).

Benthic Invertebrate Production as an Essential Variable—before *J-NABS*

Many ecological questions using secondary production as an essential response variable were addressed well before the first issue of *J-NABS*, and studies addressing these questions have continued and expanded over the years. We will consider key advances and findings in several of these research categories before discussing more recent applications of the past 25 y.

Life history and production

One of the basic types of information required for understanding the ecology of any animal is a description of its life history (**Resh and Rosenberg 2010**). The determination of life history (an account of population dynamics synchronized with life cycle) generally requires quantitative population sampling through time. As a consequence, it generates most of the data required for use in production calculations. Thus, many early and current investigators have taken advantage of this relationship and simultaneously assessed production along with life history. This practice has resulted in many descriptive studies containing detailed information about life-history variables and production. These studies often treat a single or a few taxa, and are usually entitled ''The life history and production of …'' The important relationship between life history and production was stressed in some of the early freshwater production studies (e.g., Waters and Crawford 1973, Benke 1976, Waters 1979, Elliott 1981) and in many others since the introduction of *J-NABS*, and was most recently reviewed by Huryn and Wallace (2000). One of the most important generalizations from such studies was that the ratio of cohort production to the cohort's mean biomass (cohort P/B) was ~5 (with a range of ~2 to 8), agreeing with Waters' (1969, **1987**) early theoretical analysis. Furthermore, it later became clear that annual P/B showed a strong inverse correlation with length of life. Such life history–production studies often have been the foundation for addressing other ecological questions, such as the transport of production from aquatic to terrestrial environments (e.g., **Whiles et al. 1999**, Huryn 2002). Last, the wealth of life history–production studies has been an important basis for empirical models (see History and Methods of Secondary Production above).

Comparison of populations within and among ecosystems

Another early focus of production studies was comparison of populations. Comparison of species within and among different ecosystems has often provided insight into interspecific interactions or factors affecting production. In one of the earliest studies of stream invertebrate production, Pearson and Kramer (1972) compared production of the mayfly *Baetis bicaudatus* and the caddisfly *Oligophlebodes sigma* and showed remarkable spatial and temporal constancy in a mountain spring stream over 2 y. In a longitudinal stream study, Ross and Wallace (1983) demonstrated the relative importance of different food sources to production of each of 9 caddisfly species at 6 sampling stations. Comparative studies have remained important. For example, Short

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et al. **(1987)** found substantial variation in production of the hellgrammite *Corydalus cornutus* among 4 Texas streams, with values from the Blanco River site (>13 g m^{-2} y^{-1}) among the highest ever reported for a stream insect predator. Variation in bedrock geology among streams in different regions of Alabama influenced production of the snail genus *Elimia* (**Huryn et al. 1995**) and the caddisfly *Glossosoma nigrior* (Jin and Ward 2007). Griffith et al. (**1994**) found a relationship between shredder production and pH/alkalinity in West Virginia streams. Yam and Dudgeon **(2006)** examined the influence of site and season on 2 species of atyid shrimps in 4 tropical streams. Production is a very useful variable in such comparisons because it is directly related to consumption of food resources and is a good indication of a population's relative success in different environments (Benke 2010).

Niche overlap and competition

Biotic interactions, as reflected by studies of niche overlap and competition, have been topics of considerable interest among benthic invertebrate ecologists (**Holomuzki et al. 2010**). On some occasions, production has been used to assess niche overlap and competition among coexisting species, either through overlap of resource use (as reflected in temporal overlap of production) or in field experiments. Early researchers recognized that estimation of production over short time intervals (within a year) allowed much greater understanding of population/assemblage dynamics and potential resource partitioning along the time dimension than did estimations over longer periods. Waters (1966; Fig. 1), in one of the earliest production studies of a stream invertebrate, showed that daily production of *Baetis vagans* in a small stream was highest in summer and coincided with highest drift rates. Since this early study, temporal patterns of production have been compared within assemblages of closely related species as a means of assessing temporal patterns of resource partitioning in both lentic (e.g., Benke 1976) and lotic (e.g., Georgian and Wallace 1983, Benke and Jacobi 1994, González et al. 2003, Salas and Dudgeon 2003) environments. Production also might prove to be a useful response variable in competition experiments, as demonstrated for coexisting stream snail species by Cross and Benke (2002). Although rarely used, this application appears promising.

Predator–prey relationships and the Allen paradox

Predation is another biotic interaction well studied by benthic ecologists (**Johnson et al. 1996**, **Creed 2006, Holomuzki et al. 2010**). An important aspect of predator–prey relationships is the extent to which prey production can satisfy the consumption needs of predators. High demands on macroinvertebrate production by vertebrate predators have been reported for >60 y. The observation that invertebrate biomass often seemed insufficient to support fish production became known as the Allen Paradox (Allen 1951 [Fig. 1], Hynes 1970, Waters 1988). Similar demands by invertebrate predators, such as dragonflies, also were shown (e.g., Benke 1976). One important contribution to resolution of the Allen Paradox was the eventual recognition that turnover rates of prey biomass were higher than estimated in early studies (see *Recognition of high annual P/B* below). Although the Allen Paradox also can be partially explained by consumption of hyporheic and terrestrial prey, several studies suggest that predators indeed can consume most of their prey production. Huryn (1996; Fig. 1) used a comprehensive production budget to show that brown trout (*Salmo trutta*) consumed virtually all macroinvertebrate production in a New Zealand stream and similar rates of salmonid consumption were reported for 11 of 13 streams (Waters 1988, Huryn 1996). Wallace et al. (1997b; Fig. 1) measured production by macroinvertebrate predators and prey in the same stream for 8 y and showed that predator production required essentially all prey production (Fig. 2). This pattern of high predator consumption (>80% of prey production) has been shown repeatedly for predaceous invertebrates and nonfish vertebrates in a variety of streams (Smith and

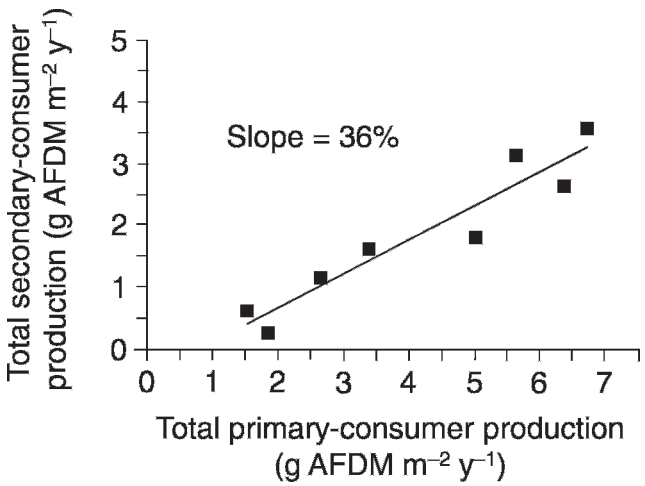


FIG. 2. Total invertebrate production plotted against invertebrate predator production over 4 y in a North Carolina stream (Wallace et al. 1997b). Slope is similar to that predicted if predator production were based on ~100% prey production. Figure redrawn from Wallace et al. (1997b with permission from the American Association for the Advancement of Science). AFDM = ash-free dry mass.

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Smock 1992, **Lugthart and Wallace 1992**, **Hall et al. 2001**, **Entrekin et al. 2007**). A unique production study of leaf beetles and their effects on water lilies showed the Allen Paradox can even be observed for plant–herbivore systems (Wallace and O'Hop 1985)! Furthermore, 41 to 64% of litterfall in a stream was necessary to support production of a single shredder species, *Pteronarcys proteus* (**Perry et al. 1987**), and large portions of leaf litter, primary production, and insect production were required to support production of tropical freshwater shrimps (Cross et al. 2008). These studies together indicate that predation (or consumption of any food resource) often results in vanishingly small surpluses of prey production (or resource supply).

The usefulness of benthic production as a response variable also was recognized in early *experimental* studies of predation, such as in the classic work of Hall et al. (1970) where both predaceous invertebrates and fish were manipulated in constructed ponds. Later field experiments, such as Rasmussen's (1987) work on effects of a predaceous leech on production of chironomid larvae in a small pond and the work of Winkelmann et al. (2007) on the effect of benthivorous fish on production of invertebrate grazers and shredders in a stream, also incorporated production as a response variable. Most predator–prey experiments in freshwaters, however, tended to ignore production of either predator or prey and the possibility that most primary consumer production is eaten by their predators. We believe that future predator–prey studies would benefit from the use of this integrative and functional variable in measuring responses.

Recognition of high annual P/B

By the mid-1970s, the maximum rate of biomass turnover (*annual* P/B) for multivoltine zoobenthos was generally thought to be ~10 (Waters 1977). At about the same time, however, other evidence (including multiple observations of the Allen paradox) suggesting much higher P/Bs was starting to appear. In particular, Mackey's (1977a, b) early work on chironomid production in English rivers suggested short life spans (<2 wk) and much higher P/Bs (>50/y) than previously envisioned. Subsequent studies in a southwestern US desert stream (Gray 1981, Fisher and Gray 1983, Jackson and Fisher 1986 [Fig. 1]) and southeastern US rivers (Benke et al. 1984 [Fig. 1], Wallace and O'Hop 1985) showed that invertebrates with short life spans (dipterans, mayflies, and beetles) could generate annual P/Bs approaching or >100/y. Although such high turnover had important implications regarding energy/nutrient flows and predator–prey interactions, its generality was unknown, and it certainly was not considered widespread. Nonetheless, additional studies of dipterans and some mayflies verified short larval life spans or high growth rates in at least subtropical and tropical streams (**Benke and Jacobi 1986, Hauer and Benke 1987**, **1991,** Stites and Benke 1989, **Jackson and Sweeney 1995,** Rosemond et al. 2001, Salas and Dudgeon 2001, Reynolds and Benke 2005, **Tronstad et al. 2007**). In several cases, this life span/growth rate information again generated annual P/Bs approaching or >100/y (e.g., Benke and Parsons 1990, Benke and Jacobi 1994, Benke 1998, **Ramírez and Pringle 1998**, 2006, Salas and Dudgeon 2003). Some studies have even indicated that growth and turnover can be relatively high in colder streams (e.g., Nolte and Hoffman 1992, **Walther et al. 2006**), but others have suggested limitation by temperature, food, O_2, habitat, or simply lower species-specific growth rates (Soluk 1985, Huryn 1990, Berg and Hellenthal 1991, **Johnson et al. 2003**, Cross et al. 2005). It is now clear that annual P/B can vary from <1 to >100/y, and investigators must be cautious in applying growth models across aquatic ecosystems of different types (see more detailed summary on high growth rates by Huryn and Wallace 2000).

Ecosystem energy flow

Early research on Cedar Bog Lake (Lindeman 1942), Silver Springs (Odum 1957), and Root Spring (Teal 1957) stand as pioneering studies of energy flow in freshwater systems. Such studies are often placed within the broader context of organic matter dynamics (**Tank et al. 2010**). Other benchmark energy flow studies soon followed in lotic environments, such as the Oconee River (Nelson and Scott 1962), the River Thames (Mann 1964), and Bear Brook (Fisher and Likens 1973; Fig. 1). Although these early studies used relatively crude methods for estimating secondary production, they paved the way for far more detailed studies of total benthic production and energy flow, particularly during the 1980s, that used increasingly more exact approaches (e.g., Fisher and Gray 1983, Krueger and Waters 1983, Benke et al. 1984, Smock et al. 1985 [Fig. 1], Jackson and Fisher 1986, Huryn and Wallace 1987 [Fig. 1]; see more complete reviews in Benke 1993, Poepperl 1999, Meyer and Poepperl 2003). In several cases, production by different functional feeding groups was evaluated, but recent work has been more fine-tuned in quantifying the trophic basis of production for individual species and in the development of quantitative food webs.

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Trophic basis of production

Benke and Wallace (1980; Fig. 1) used an assemblage of filter-feeding caddisflies to estimate the relative contribution of different food types to production of a given species by combining production, diet information, and food-specific assimilation efficiencies. This *trophic basis of production* was not necessarily the same as that suggested by diet alone because it accounted for food-specific assimilation efficiencies. Such analyses allowed them to determine, for example, that production of these omnivorous caddisflies was based primarily on animal prey rather than on detritus or algae. Similar studies on other caddisfly assemblages soon followed (Haefner and Wallace 1981, Ross and Wallace 1981, 1983, Parker and Voshell 1983). Smock and Roeding (1986) were the first to apply the approach to an entire macroinvertebrate assemblage at multiple sites in a South Carolina stream and showed that, contrary to their functional group categorization, a high fraction of scraper production was from eating fine particulate organic matter and a high fraction of shredder production was from eating algae. The collective conclusion from these early studies was that estimating the contribution of food sources to production of individual species provides a much finer-scale analysis of resource use than does simply grouping invertebrates into functional feeding groups. The approach has been used subsequently to quantify the contributions of various food sources to production of *individual* taxa (e.g., Johnson et al. 2000, Collier et al. 2004, Alvarez and Pardo 2005, Cereghino 2006, Yan and Li 2006b), *taxonomic groups* (e.g., Petersen 1989, **Roeding and Smock 1989**, Smith and Smock 1992, Benke and Jacobi 1994, Sanchez and Hendricks 1997, **Evans-White et al. 2003**, Salas and Dudgeon 2003, Yan and Li 2006a), and entire *invertebrate assemblages* (e.g., **Lugthart and Wallace 1992**, **Hall et al. 2001**, **Carlisle and Clements 2003**).

Habitat-specific microdistributions

The importance of habitat heterogeneity and patch dynamics is well recognized in studies of freshwater benthic invertebrates (**Townsend 1989**, **Winemiller et al. 2010**) and has been considered at both fine (microdistribution) and coarse scales (see *Habitat-specific macrodistributions* below). One of the earliest attempts to consider habitat (or patch)-specific processes in freshwaters was assessment of habitat-specific production. Invertebrate production and its distribution among species and functional groups is a direct reflection of habitat-specific resource consumption and processing rates. In an early microdistribution paper, Resh (1977) showed that production of the stream caddisfly *Ceraclea ancylus* increased from water willow (*Justicia)* to pool to riffle habitat and speculated that the increase reflected increased particle sizes and availability of food resources. Secondary production analyses were used in studies by Cudney and Wallace (1980), Benke et al. (1984, 1985), and Smock et al. (1985, 1989) to demonstrate the importance of submerged wood (snags or debris dams) as a habitat in Coastal Plain streams (review by Benke and Wallace 2003). Gladden and Smock (1990) estimated production in a stream–floodplain ecosystem and found that, after taking floodplain area into account, production was 1 to 2 orders of magnitude higher in the floodplain than in channels. Huryn and Wallace (1987) were the first to quantify invertebrate production among riffle, pool, and bedrock habitats in a high-gradient stream. Distribution of invertebrates in the hyporheic zone (**Boulton et al. 2010**) adds a vertical element of microdistribution, but only a few attempts have been made to assess depth-specific production. Smock et al. (1992) estimated the vertical distribution of production in a sandy-bottom Virginia stream and found that while 79% of production was in the top 5 cm, only 32% was actually at the surface (<1 cm). Huryn (1996) incorporated the explicit measurement of production by hyporheic fauna into an energy budget used to assess the Allen Paradox in a New Zealand stream and found that while 84% of production was in the top 10 cm, the remainder occurred in sediments 10 to 40 cm deep. In contrast, studies in another New Zealand stream showed that >76% of production of 2 insect species was distributed at depths >10 cm below the surface (Collier et al. 2004, Wright-Stow et al. 2006). These and many other studies have demonstrated that knowledge of the distribution of production among microhabitats greatly enhances our understanding of habitat-specific processes in aquatic systems (e.g., Wohl et al. 1995, **Pickard and Benke 1996**, Poepperl 1996, Dudgeon 1999, Buffagni and Comin 2000, Reynolds 2002, Chadwick and Huryn 2007, **Babler et al. 2008**).

Effects of pollution

Although *structural* measurements of benthic assemblages (e.g., species diversity) have been used widely in pollution assessment (**Dolédec and Statzner 2010, Hawkins et al. 2010**), secondary production has been regarded as a measure of *functional* impact since the 1970s, particularly for enriched streams (e.g., see brief reviews of this early literature in Benke 1984, 1993, Bonada et al. 2006). Pollution can provide a resource subsidy (increasing production) or act as a physiological stressor (decreasing production). Recent studies based on comparative and experimental

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approaches have become more specific in describing pollution effects on production among species, functional groups, and foodweb flows. Wallace and colleagues (Lugthart et al. 1990, **Lugthart and Wallace 1992**, Chung et al. 1993, Whiles and Wallace 1995) examined effects of the pesticide methoxychlor on species and functional-group production in small streams in North Carolina. In general, they found that production gave a more complete picture of assemblage dynamics during disturbance and subsequent recovery than did abundance or diversity. Wallace et al. (1996; Fig. 1) later used production data from their pesticide experiment to help validate use of 2 biotic indices as reasonable indicators of changes in ecosystem processes. In a more recent experiment in the same streams, nutrient-induced changes in the detrital/microbial food base resulted in significant taxon-specific increases in invertebrate production, demonstrating the importance of food quality to fast-growing detritivores (Cross et al. 2005, 2006). Similarly, growth and production of chironomids are very sensitive to P increases in Costa Rican streams (Ramírez and Pringle 2006).

Several recent studies have used invertebrate production to assess effects of pollutants from sources including heavy metal contamination (**Carlisle and Clements 2003**, 2005, Woodcock and Huryn 2007), acid-mine drainage (Hünken and Mutz 2007), roadways (Woodcock and Huryn 2008), and urban sewage contamination (deBruyn et al. 2003). Runck (2007) studied a stream that was simultaneously enriched and Hg-contaminated and found that high production was concentrated in a single chironomid genus. Buffagni and Comin (2000) studied a relatively unimpacted stream, but suggested that comparison of habitat-scale rank/production curves could be useful in assessment of ecological integrity. In contrast, **De Lange et al. (2004)** suggested that invertebrate production at moderate levels of pollution in floodplain creeks affected assemblage structure but not production. Production only recently has been considered as a response to thermal pollution, such as from power plant effluents or climate change (Cid et al. 2008, Winterbourn et al. 2008). Studies based on both invertebrate assemblage structure and production clearly provide a more complete picture of degradation in freshwater systems than either by itself.

Effects of dams

Dam construction and operation is just one type of anthropogenic physical disturbance to streams (**Stanley et al. 2010**), but it is pervasive and a disturbance to which invertebrates are highly sensitive. It has been known for at least 5 decades that filter-feeding invertebrates are often extremely abundant at lake outlets, but it was measurement of their secondary production that drove this point home. Production of filtering collectors, such as net-spinning caddisflies (MacFarlane and Waters 1982, Parker and Voshell 1983) and black flies (Gíslason and Gardarsson 1988, Wotton 1988), is typically very high below dams with relatively stable flows. These estimates represented some of the highest ever recorded. Production by other taxa, such as mayflies (MacFarlane and Waters 1982, **Rader and Ward 1989**) and stoneflies (Helešic and Sedlák 1995), might be enhanced as well, whereas other groups, such as chironomids, might not be affected (Grzybkowska et al. 1990). Determining cause and effect for increased production is not always successful because temperature, flow regimes, food supply, and habitat type are all affected in streams below dams. Nonetheless, extremely high values for filtering collectors are often attributed to the plankton food subsidy from the upstream impoundment, and production often decreases rather rapidly downstream as the subsidy becomes depleted by consumers (e.g., Parker and Voshell 1983, Poepperl 1999). This phenomenon is not restricted to dams on large rivers because Mackay and Waters (1986) showed a clear pattern of enhanced hydropsychid production below dams in a small stream. However, high levels of invertebrate production below dams are by no means the rule (e.g., Fjellheim et al. 1993) because of extreme alterations in flow regime from hydropower, regulation, or diversions.

Linkages between aquatic and other ecosystems

The transfer of energy and matter from terrestrial to freshwater systems (particularly to streams) has been widely known for many years (Cummins 1974, **Tank et al. 2010**). The reverse movement from aquatic to either adjacent terrestrial systems or distant aquatic systems has not been as well recognized, but is a question of considerable current interest (Baxter et al. 2005, **Lamberti et al. 2010**). Early estimates of aquatic-to-terrestrial transfers took the form of ratios of emergent insect biomass to secondary production and have been done for >70 y (see table 6 in Jackson and Fisher 1986). Thus, secondary production analysis was at the forefront of quantifying the transfer of animal biomass from aquatic to terrestrial food webs. Jackson and Fisher (1986) estimated that an incredible 23 g DM m^{-2} y^{-1} was transferred from Sycamore Creek to the adjacent terrestrial ecosystem from insect emergence, whereas only 3% returned for oviposition. This transfer represented roughly 17% of total

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secondary production. Other studies have found that emergent production is often not nearly as high as was found by Jackson and Fisher (e.g., Gray 1989, **Stagliano et al. 1998**, **Whiles et al. 1999**, Whiles and Goldowitz 2001, Huryn 2002), but it still can be an extremely important source of prey for riparian insectivores, such as spiders, birds, and bats (**Fisher 1991**). In another version of such transfers, Register et al. (2008) estimated that pond salamanders consumed up to 16 g ash-free dry mass (AFDM) m^{-2} y^{-1} of prey (mostly invertebrates) and that they exported 3 to 8% of this consumption (0.30–0.85 g m^{-2} y^{-1}) to the terrestrial environment in the form of emigrating salamander biomass. Thus, production estimates can be used to help analyze intersystem transfers in several ways.

Benthic Invertebrate Production as an Essential Variable—after *J-NABS*

Many of the ecological questions addressed using production before *J-NABS* continue to be pursued actively today, but a diversity of new applications has appeared within the past 25 y; these applications offer a glimpse into the future.

Habitat-specific macrodistributions

Interest in the *microdistribution* of production clearly began before *J-NABS*; studies of the *macrodistribution* of production primarily came later. A major interest in invertebrate macrodistribution was associated with a central prediction of the River Continuum Concept (RCC) of Vannote et al. (1980): a synchronous shift in type of food resources and functional feeding group composition from the head to the mouth of a river system. However, most studies that initially tested this prediction used macroinvertebrate *abundance* as the metric (e.g., Hawkins and Sedell 1981, Minshall et al. 1983). Benke (1993) and Webster et al. (1995) both suggested that a *functional* metric, such as secondary production, was more appropriate for questions concerning ecosystem function, and they each used meta-analytical approaches to test the RCC predictions. Benke used the world literature (Fig. 3A, B), and Webster et al. used studies from the eastern US. Both found that stream assemblages showed patterns of relative production among functional groups that generally supported RCC predictions, but to different degrees than patterns found using abundance. For example, relative scraper production peaked in mid-reaches, but it did not dominate production as suggested by the RCC (Fig. 3A). Relative production of filtering collectors increased with stream size as suggested by the RCC, but was dominant or codominant with production by gatherers in downstream reaches. These trends were for site-specific *relative* production; total production (not predicted by RCC) increased greatly with stream size (Fig. 3B). Grubaugh et al. (1997) found similar results in a single river system, the Little Tennessee (Fig. 3C, D). One difference in their results, compared to Benke (1993) and Webster et al. (1995), was higher relative production of filtering collectors in small streams (Fig. 3C), but these were primarily caddisflies that consumed drifting prey rather than detritus particles. Rosi-Marshall and Wallace (2002; Fig. 1), also working on the Little Tennessee River, estimated changes in food *consumption* along the continuum, further illuminating functional aspects because actual food consumed was not necessarily consistent with functional group classification. Clearly, the macrodistribution of invertebrate production and consumption along the river continuum provides greater insight into functional changes than do abundance data alone.

Production studies in *atypical* aquatic habitats also might be considered to fall within the macrodistribution category. These systems include the ecologically and physiologically challenging; e.g., saline streams and rivers (Chadwick and Feminella 2001, Barahona et al. 2005); acid streams (Pretty et al. 2005); temporary streams, pools, and floodplains (Gladden and Smock 1990, Huryn 2002, Alvarez and Pardo 2005, Chadwick and Huryn 2007); and streams subject to severe scouring (Jackson and Fisher 1986). They also include apparently benign habitats, such as certain lake outlets (Poepperl 1996), and thermally and hydrologically constant, travertine spring-ponds (**Runck and Blinn 1990**, **1993**, Dehdashti and Blinn 1991). These atypical habitats span some of the lowest and highest annual secondary production values yet recorded for streams, and thus, represent how function varies across a freshwater landscape.

Effects of catchment land use

The importance of landscape features to stream ecosystems was known well before the first issue of *J-NABS* (**Johnson and Host 2010**). Almost all studies using secondary production as a response variable for explicit assessment of the effects of catchment land use (nonpoint pollution) on stream assemblages began after the inception of *J-NABS*. Some of the earliest studies involved effects of forest disturbance and tended to show that production of some species typically increased with disturbance (Haefner and Wallace 1981, Wallace and Gurtz 1986, Stout et al. 1993). Other landuse studies addressed the influence of agriculture or agricultural practices (Sallenave and

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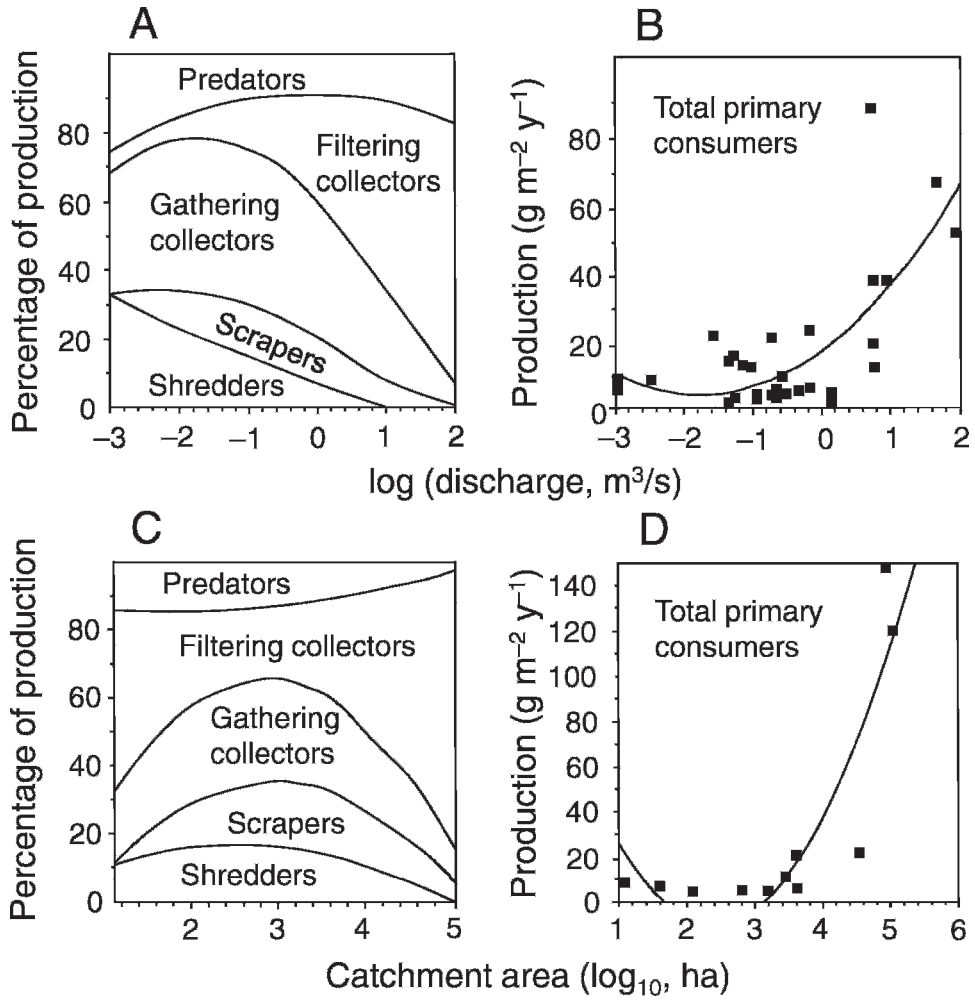


FIG. 3. Relative production (percentage of P) (A, C) and total production fitted to a 2nd degree polynomial (B, D) of functional feeding groups along a river continuum from a meta-analysis by Benke (1993) (A, B) and the Little Tennessee River (Grubaugh et al. 1997) (C, D). Composite figures redrawn from Benke (1993), with permission from the International Society of Limnology, and data in Grubaugh et al. (1997).

Day 1991, Sanchez and Hendricks 1997). Perhaps the most notable such study was that of Grubaugh and Wallace (1995) who assessed effects of landuse change from agriculture to fallow on the production ecology of an extensive bedrock shoal in a Georgia Piedmont river over a 35-y span. More recent studies have continued to include production analysis to assess effects of logging (Kedzierski and Smock 2001), agricultural/urban land use (**Shieh et al. 2002**, 2003, Pollock 2008), and even atmospheric N and S deposition (Chadwick and Huryn 2005; Fig. 1). Measuring shifts in absolute and relative production of functional and taxonomic groups should continue to provide a useful indication of functional impacts from catchment changes (where the actual pollutant is impossible to pinpoint), just as for point-source pollutants.

Quantitative food webs

Building on their *trophic basis of production* approach using production and diet analysis (see *Trophic basis of production* above), Benke and Wallace (1997) estimated ingestion flows in developing a quantitative food web for snag-dwelling caddisflies in a Georgia river. They suggested that such *quantification* of flows could be used as a measure of *linkage strength* and provided greater understanding of food webs than connectance approaches. In this and a subsequent analysis of predaceous species (Benke et al. 2001), ingestion flows in this single snag food web varied by >1000×, omnivores consumed more prey than did strict predators, and trophic position of predators varied from 2.3 (omnivores) to 3.5 (top invertebrate predator), where a value of 2.0 would be for a primary consumer. Several others

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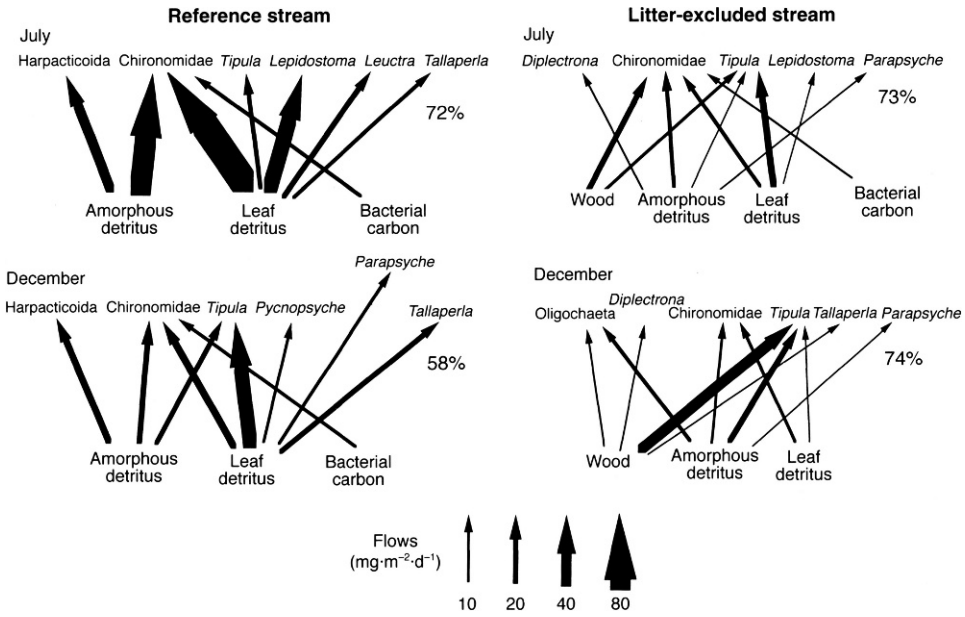


FIG. 4. Quantitative food webs during 2 seasons in a reference stream and a litter-excluded stream in North Carolina (from Hall et al. 2000, with permission from The Ecological Society of America). Thickness of lines approximates magnitude of daily flows.

have now quantified foodweb flows in this way; e.g., Shieh et al. (**2002**) working at 3 differentially impaired sites on the Colorado River, Rosi-Marshall and Wallace (2002) in a mountain stream continuum in North Carolina, Liu et al. (2006) in a macrophyte-dominated lake in Hubei Province (China), Runck (2007) on an industrially contaminated stream in Tennessee, Cross et al. (2007; Fig. 1) in nutrient-enriched vs nonenriched North Carolina streams, and Register et al. (2008) in 4 ponds where invertebrate flows to predaceous amphibian larvae were quantified. Stagliano and Whiles (**2002**) and Entrekin et al. (**2007**) followed a similar approach for streams in Kansas and the Upper Peninsula of Michigan, respectively, but used functional feeding groups without actual diet analysis. Poepperl (2003) and Meyer and Poepperl (2004) also created quantitative food webs using production from German stream and lake-outlet communities with a somewhat different approach. Last, Woodward and Hildrew (2002) and Woodward et al. (2005) have provided thought-provoking discussions on different foodweb approaches in streams, including the trophic basis approach of Benke and Wallace. Quantitative foodweb analysis is clearly a topic of growing interest in freshwater ecosystems.

Experimental and tracer-based studies of the trophic basis of production

Perhaps the most powerful study assessing the trophic basis of production in stream invertebrate assemblages was the pioneering work of Wallace et al. (1997b, 1999). This work was a continuation of long-term studies at the Coweeta Hydrologic Laboratory (**Wallace et al. 1997a**), and was one of the many attempts to describe stream organic matter budgets worldwide (**Webster and Meyer 1997**, **Tank et al. 2010**). Wallace and colleagues experimentally decoupled a headwater stream community from its putative energy source with a mesh canopy and riparian barriers to exclude litter inputs for 4 y. Weighted secondary production for riffle, run, and pool habitats declined to 22% of pretreatment levels by the 4th year of treatment and was among the lowest reported for stream invertebrates. A strong relationship between litter inputs and production unambiguously demonstrated strong bottom-up control of production and explicitly supported the long-held assumption that autumn-shed leaves were the foundation for production in forested, headwater streams. Using the same experiment, Hall et al. (2000; Fig. 1) showed dramatic changes in the largest taxon-specific foodweb flows from detritus and bacteria to invertebrates (Fig. 4), and found similarly dramatic changes in largest flows from invertebrate prey to predators. Another notable approach to assessing the trophic basis of production was that of McCutchan and Lewis (2002; Fig. 1), who combined estimates of macroinvertebrate production with natural abundance stable-isotope ratios (C, N) to assess the relative contributions of terrestrial and aquatic primary production to consumer biomass in

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North St Vrain Creek, Colorado. They found that the contribution of aquatic primary production to consumer production (40–80%) was much higher than suggested by its availability (<2–40% of available organic matter input).

Chemical flows and stoichiometry

Nutrient dynamics have been of interest to stream ecosystem ecologists for many decades (**Mulholland and Webster 2010**), but only within the past 2 decades has secondary production been recognized as useful in quantifying chemical flows. Grimm (1988) appears to have been the first to use invertebrate production, or daily P/B (from Fisher and Gray 1983, and Jackson and Fisher 1986), to estimate N flows (ingestion and incorporation). She found that invertebrates played a major role in the N budget of a Sonoran desert stream. However, it was not until much more recently that production became a more common tool for estimating the role of invertebrates in nutrient dynamics. Hall et al. (2003) used production estimates to develop a N budget in a Wyoming stream dominated by the nonnative New Zealand mud snail and showed these snails accounted for ⅔ of NH_4^+ demand by autotrophs. Runck (2007) converted energy flows in the food web of his industrially contaminated stream to Hg flows from periphyton to chironomids and from the aquatic to terrestrial environment through emergence. Cross et al. (2007) also used production to estimate annual flows of C, N, and P in enriched and nonenriched streams, and were among the first to recognize how stoichiometric properties (i.e., ratio of elements, C:N:P) might affect stream production and quantitative food webs. Singer and Battin (2007) also identified the importance of stoichiometric relationships when they combined stable isotope analysis with secondary production in assessing the influence of sewage-derived particulate organic matter in an Austrian stream. These recent studies have greatly reinforced the potential of production analyses in quantification of nutrient flows in future work.

Effects of nonnative species

Introduction of nonnative organisms to stream ecosystems could greatly influence invertebrate production and other functional properties of aquatic ecosystems, although this effect might be difficult to demonstrate because of lack of preinvasion data. The first assessments of the impact of nonnative species in streams using production as the response variable occurred almost 60 y ago (i.e., trophic support for introduced brown trout in New Zealand; Allen 1951) and were focused on enhancing the *success* of invaders rather than assessing their negative effects. However, explicit experimental assessments of effects of invaders on production have occurred much more recently. Huryn (1998; Fig. 1) used a natural experiment to compare production patterns of 2 adjacent New Zealand streams. Brown trout were introduced to one stream before the early 20th century, whereas an intact native community was maintained in the other. Production analyses showed that a trophic cascade was induced by efficient top-down control of invertebrates by trout but not by native fishes. A similar approach was used by Anderson and Rosemond (2007) who assessed the effect of a nonnative ecosystem engineer—the North American beaver (*Castor canadensis*)—on the production ecology of Chilean stream invertebrates.

Invasive mollusks have been particularly prominent in production-focused studies of benthic ecology. The Asiatic clam, *Corbicula fluminea,* colonized much of the US during the 20th century. Its production has been >20 g DM m^{-2} y^{-1} in some locations, presumably enough to affect other invertebrates (e.g., Aldridge and McMahon 1978, Marsh 1985), although not always (Stites et al. 1995). Hall et al. (2003, 2006) studied the New Zealand mudsnail (*Potamopyrgus antipodarum)* in multiple streams in the Greater Yellowstone area of Wyoming and showed that mudsnails dominated invertebrate assemblages with production sometimes as high as 200 g m^{-2} y^{-1}. The irony of New Zealand acting as a sort of nexus for studies of the production ecology of invasive species—trout or snails—can hardly pass unmentioned! No consideration of invading mollusks would be complete without mention of the zebra mussel (*Dreissena polymorpha*). Karatayev and Burlakova (1995) showed a dramatic effect of zebra mussels on primary and secondary production in Lukomskoe Lake, Belarus, with a decrease in zooplankton production and increases in both benthic and fish production. Johannsson et al. (2000) found a somewhat similar result after dreissenid mussels invaded Lake Erie and reduced planktonic primary and secondary production, but did not reduce production of other benthos.

Metabolic theory

Recent studies of the role of metabolic scaling in constraining bioenergetic relationships between consumer body size and the components of production (e.g., abundance, biomass, individual growth rate, P/B) differ somewhat from earlier empirical studies (e.g., Banse and Mosher 1980, **Morin 1997**). This *metabolic theory*, as summarized by Brown et al. (2004), uses a first-principle approach to derive specific

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predictions about the relationships between individual mass (M) and ecological variables operating at different scales. The theory is grounded on the assumption that processes driven by metabolism at all ecological scales are subject to ¼-power scaling and that individual metabolism scales as $M^{0.75}$ because of the fractal-like architecture of internal distribution systems. Huryn and Benke (2007; Fig. 1) used the metabolic-theory approach as a predictive framework for assessing the specific relationship between body size, abundance, biomass, production, and P/B for stream animal communities. Although exceptions were found, scaling exponents describing the relationship between P/B, production, and body size for selected temperate stream assemblages (e.g., Fig. 5) showed concordance with the ¼-power scaling relationships for 3 of 4 stream communities. Tagliapietra et al. (2007) even suggested that equations from metabolic theory could be applied for indirect estimation of secondary production, although such estimates would incur considerable error (Huryn and Benke 2007). Applications of metabolic theory to stream communities and incorporation of production, P/B, and growth rates as independent variables are largely unexplored topics that might prove to be very interesting.

Benthic meiofauna vs macrofauna

The relative importance of meiofauna (individuals that pass through a 500-µm sieve) vs macrofauna in terms of community and ecosystem processes has concerned benthic ecologists for decades (Hakenkamp and Morin 2000, Hakenkamp et al. 2002). Early attempts were made to estimate production of freshwater meiofauna with empirical models (e.g., Strayer and Likens 1986, Morin et al. 1995), but their overall contribution to energy flow in freshwater food webs remains poorly understood, primarily because of problems with methods rather than lack of interest. Strayer and Likens (1986) estimated ~50% of total benthic production in a New Hampshire Lake was contributed by meiobenthos, whereas Morin et al. (1995) estimated only ~3% of benthic production was contributed by animals <1 mm length in several streams of eastern Canada. Hakenkamp and Morin (2000) used an analysis of assemblage size spectra of several streams to conclude that meiofauna probably contribute <5% to total metazoan production and, thus, are minor contributors to stream secondary production. In contrast, Stead et al. (2005) estimated production of benthic fauna in an English acid stream and found that 15% was attributable to *permanent* meiofauna (e.g., taxa *always* small enough pass through a 500-µm mesh) and an additional 36% was attributable to *temporary* meiofauna (early stages of taxa usually small enough to pass through a 500-µm mesh). In an English chalk-stream, Tod and Schmid-Araya (2009) estimated meiofauna to contribute 7 to 8% of production by benthic fauna in a highly productive system (65 $g\ m^{-2}\ y^{-1}$). Detailed species-specific production studies of benthic microcrustaceans (meiofauna for much of their life) have been conducted in 2 southeastern US wetlands (Gladden and Smock 1990, **Lemke and Benke 2004**, 2009) and in the Thames River, UK (Robertson 1995). Annual production often approached or was >1 $g\ m^{-2}\ y^{-1}$. In an Alabama wetland, production of a 32-species microcrustacean assemblage (benthic, planktonic, epiphytic combined) was >12 $g\ m^{-2}\ y^{-1}$, a result implying significant contributions to total benthic production (Lemke and Benke 2009). Clearly, results from these studies allow no single conclusion to be drawn about the relative importance of meiofauna, but further work on production seems justified if their role in ecosystem processes is to be understood. Biomass is almost universally lower for meiofauna than macrofauna, and the question is whether the P/B of meiofauna can be sufficiently high to make meiofauna production a significant component.

Biodiversity vs ecosystem function

Much current emphasis in ecology, including in aquatic communities, has been placed on the relationship between biodiversity and ecosystem function (e.g., Giller et al. 2004). Given that secondary production is an aspect of ecosystem function, a seemingly useful analysis would be to explore the relationship between aquatic macroinvertebrate diversity (or richness) and their production. It is surprising that so little has been done because production and richness can be measured simultaneously. As far as we are aware, Statzner and Resh (1993) were the first to address this question when they analyzed an historical data set from streams in Austria and Germany. They used an established relationship between Ephemeroptera, Plecoptera, Trichoptera (EPT) biomass of insect emergence and benthic production (a shortcut approach) and found a significant relationship between EPT emergence biomass and EPT richness for total EPT, gathering collectors, and predators, but not for grazers, shredders, or filtering collectors. Statzner and Lévêque (2007) later examined a much larger literature on invertebrate production and richness in streams and found equivocal support for a production–diversity relationship after conducting a variety of analyses. Although the equivocal results of these 2 studies were

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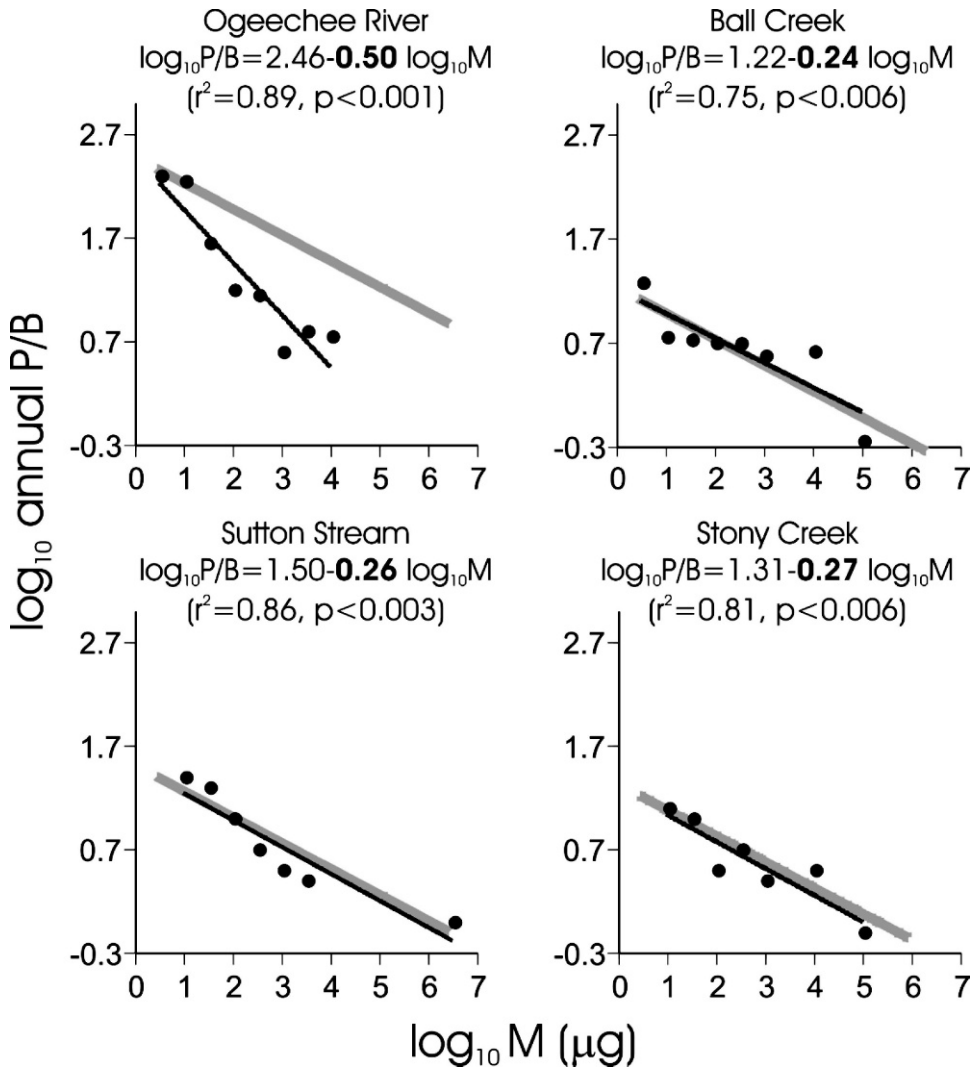


FIG. 5. Log–log plots of annual production/biomass (P/B) against individual mass (M; μg dry mass/individual) for 4 stream communities. The grey line indicates the predicted slope of the relationship between log(P/B) and log(M) ($P/B \propto M^{-0.25}$) based on metabolic theory. The black line indicates the slope derived from least-squares regression of the data. From Huryn and Benke (2007).

not encouraging, Statzner and Lévêque (2007) readily acknowledged that confounding environmental factors can overwhelm any relationship that might exist between production and diversity in their meta-analyses. We suggest that the greatest chance of success in tests of production–diversity relationships for aquatic invertebrates would be for studies designed with that specific purpose in mind. For example, Whiles and Goldowitz (2001) showed a positive relationship between emergent insect production and diversity in a Platte River wetland under different hydrologic regimes, and Pollock (2008) recently demonstrated consistent and positive relationships between invertebrate production and diversity using Hester–Dendy samplers in 21 urban streams (Atlanta, Georgia) and 15 relatively natural streams (Alabama) in the southeastern US. Production–diversity results in systems under human influences (e.g., organic pollution or below dams) are likely to differ substantially from these results, but this area seems to be an important one for future research.

Future Directions

Secondary production must be recognized for what it is—a bioenergetically based growth process that can be quantified to produce a currency or variable that describes this process (e.g., $g\ m^{-2}\ y^{-1}$). Thus, considering the *future* of secondary production research is no different than considering future applications of

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other variables, such as population *density* or *biomass*. Future application of any one of these measures depends on the types of questions asked, and a key to understanding future questions is to examine the nature of those asked in the past. Although secondary production is still woefully underused, the studies summarized above illustrate that it is becoming used for a much wider diversity of questions in benthic ecology than in the past. This increasing momentum should result in more widespread use of production estimates than its surrogates, density and biomass. This trend is as it should be—a variable should be chosen for its explanatory power rather than its ease of quantification. The improvement and standardization of production techniques has relieved much of the toil originally required and appears at least partly responsible for more frequent routine use of production. A potential downside to the increasing use of production statistics is blind application of empirical or theoretical models as shortcut approaches. The assumptions involved in their use should be carefully weighed against their advantages. Last, we suggest that perhaps the best evidence that production biology has matured is the absence of ''production'' in titles of recent innovative papers. Whereas measurement of production was in itself worthy of publication a few decades ago and was usually prominently included in titles, production might now be viewed as a variable that often has less intrinsic value than the questions it is being used to address. Such questions include many of those introduced since the inception of *J-NABS*, such as foodweb analysis, chemical flows and stoichiometry, experimental and tracer-based field studies on resource use, effects of human interventions, metabolic theory, and richness/function relationships. Future applications ultimately should be determined by whether investigators think that secondary production can better facilitate answers to ecological riddles than can density and biomass.

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