LIFE HISTORY AND PRODUCTION OF STREAM INSECTS

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Abstract Studies of the production of stream insects are now numerous, and general factors controlling the secondary production of stream communities are becoming evident. In this review we focus on how life-history attributes influence the production dynamics of stream insects and other macroinvertebrates. Annual production of macroinvertebrate communities in streams world-wide ranges from approximately $10^0$ to $10^3$ g dry mass m$^{-2}$. High levels are reported for communities dominated by filter feeders in temperate streams. Filter feeding enables the accrual and support of high biomass, which drives the very highest production. Frequently disturbed communities in warm-temperate streams are also highly productive. Biomass accrual by macroinvertebrates is limited in these streams, and production is driven by rapid growth rates rather than high biomass. The lowest production, reported for macroinvertebrate communities of cool-temperate and arctic streams, is due to the constraints of low seasonal temperatures and nutrient or food limitation. Geographical bias, paucity of community-wide studies, and limited knowledge of the effects of biotic interactions limit current understanding of mechanisms controlling stream productivity.

INTRODUCTION

Insects and other macroinvertebrates play a central role in the flow of materials and energy through most terrestrial and benthic freshwater food-webs (reviews in 120, 124, 144). Their quantitative influence on this flow will be largely defined by the magnitude of their production. Production at a given trophic level sets limits for productivity of higher trophic levels, while simultaneously affecting rates of resources removed from lower levels. Details of this interactive process are poorly understood for most macroinvertebrate communities (107). However, it is becoming increasingly apparent that this process is an important determinant of overall ecosystem productivity (62).
We agree that production "by itself does not tell us much about the influence of invertebrates on ecosystem functioning since it is only one end product of organic matter processing" (39:1217). However, we emphasize that, when combined with information about food-web interactions (sensu 100), a comprehensive knowledge of production will improve understanding of the structure and function of both communities and ecosystems (15, 107). For stream communities in particular, estimates of macroinvertebrate production have recently been used to quantify the consequences of direct consumption and cascading trophic interactions to total stream primary productivity (64, 65), and to indicate the importance of a given food-web link or trophic resource to overall ecosystem function (15, 53).

Secondary Production and Life History

In general use, "secondary production" refers to the formation of animal biomass over time (mass area$^{-1}$ • time$^{-1}$; review in 8). Annual secondary production, for example, is the sum of all biomass produced by a population during one year, including production remaining at the end of the year and all biomass produced during this period. Losses may include mortality (e.g. disease, parasitism, cannibalism, and predation), loss of tissue reserves (e.g. molting, silk, and starvation), and emigration. The secondary production of a population (P) is the product of the biomass-specific growth rate (g, mass$^{-1}$ • mass$^{-1}$ • time$^{-1}$) and population biomass (B, mass$^{-1}$ • area$^{-1}$) (P = g × B; review in 8). Numerous methods exist for measuring secondary production, and the relationship between the biomass-specific growth rate and population biomass is implicit to all (7).

The contrasting roles of growth rate and biomass in determining production are conveniently summarized by the P/B ratio. Cohort P/Bs for stream macroinvertebrates usually range from two to eight (7, 148). Annual P/Bs for entire communities, however, range from less than 1-117 because some populations may complete more or less than one cohort each year (8). The annual and daily P/B provides an index allowing comparison of growth rates (i.e. g = P/B) among populations and communities, and will be used as such throughout this review (e.g. Tables 1 and 2).

Rates of biomass growth and accrual for any macroinvertebrate population are constrained by "life history"—the temporal pattern of development from egg through adult stages and the duration and abundance of each stage (25). Natality, abundance, individual growth rate, individual biomass, dispersal, and survivorship are all important life-history attributes that together determine levels of production at the population level (7, 8). Because of the close relationship between life-history attributes and production, patterns of production among macroinvertebrate populations and communities must also reflect the relationship between life history and the environmental template (129).

The general objective of this review is to address the relationship between life-history attributes and production by freshwater macroinvertebrate communities.
<table>
<thead>
<tr>
<th>Organism</th>
<th>Growth rate (day$^{-1}$)</th>
<th>Annual P/B</th>
<th>Developmental period</th>
<th>Habitat/location</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Low Growth Rates</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Unio tumidus</em> (Unionacea)</td>
<td>0.00001–0.00016 $^a$</td>
<td>0.004–0.057</td>
<td>10+ years?</td>
<td>lake/Hungary</td>
<td>108</td>
</tr>
<tr>
<td><em>Unio tumidus</em> (Unionacea)</td>
<td>0.0004$^a$</td>
<td>0.13</td>
<td>12 years</td>
<td>river/England</td>
<td>94</td>
</tr>
<tr>
<td><em>Austropotamobius pallipes</em> (Decapoda)</td>
<td>0.0009$^a$</td>
<td>0.32</td>
<td>11 years</td>
<td>stream/England</td>
<td>18</td>
</tr>
<tr>
<td><em>Chironomus</em> (Diptera)</td>
<td>0.0013$^a$</td>
<td>0.49</td>
<td>7 years</td>
<td>tundra pools/Alaska</td>
<td>23</td>
</tr>
<tr>
<td><em>Lara avara</em> (Coleoptera)</td>
<td>0.0031–0.0036$^b$</td>
<td>1.1–1.3$^c$</td>
<td>5–6 years</td>
<td>stream/Oregon</td>
<td>131</td>
</tr>
<tr>
<td><em>Acroneuria lycorias</em> (Plecoptera)</td>
<td>0.0039–0.0043$^a$</td>
<td>1.4–1.6</td>
<td>3 years</td>
<td>stream/Michigan</td>
<td>34</td>
</tr>
<tr>
<td><em>Sericostoma personatum</em> (Trichoptera)</td>
<td>0.0066$^a$</td>
<td>2.4</td>
<td>3 years</td>
<td>stream/Denmark</td>
<td>72</td>
</tr>
<tr>
<td><em>Philocosca alba</em> (Trichoptera)</td>
<td>0.0079$^b$</td>
<td>2.9$^c$</td>
<td>3 years</td>
<td>stream/Alberta</td>
<td>93</td>
</tr>
<tr>
<td><em>Hexagenia limbata</em> (Ephemeroptera)</td>
<td>0.0082$^d$</td>
<td>3.0$^c$</td>
<td>3–4 years</td>
<td>reservoir/Manitoba</td>
<td>44</td>
</tr>
<tr>
<td><em>Euthyplocia hecuba</em> (Ephemeroptera)</td>
<td>0.012–0.014$^b$</td>
<td>4.4–5.1$^c$</td>
<td>22 months</td>
<td>stream/Costa Rica</td>
<td>137</td>
</tr>
<tr>
<td><strong>High Growth Rates</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Diamesa incallida</em> (Diptera)</td>
<td>0.17–0.22$^c$</td>
<td>62–80$^c$</td>
<td>35–45 days</td>
<td>stream/Germany</td>
<td>96</td>
</tr>
<tr>
<td><em>Baetis</em> spp. (Ephemeroptera)</td>
<td>0.265$^a$</td>
<td>97</td>
<td>19 days</td>
<td>stream/Georgia</td>
<td>11</td>
</tr>
<tr>
<td><em>Polypedilum epomis</em> (Diptera)</td>
<td>0.29$^a$</td>
<td>106$^c$</td>
<td>22 days</td>
<td>stream/Costa Rica</td>
<td>75</td>
</tr>
<tr>
<td><em>Chironomidae</em> (Diptera)</td>
<td>0.33$^a$</td>
<td>120</td>
<td>12 days</td>
<td>stream/Arizona</td>
<td>74</td>
</tr>
<tr>
<td><em>Orthocladius calvus</em> (Diptera)</td>
<td>0.56$^b$</td>
<td>203$^c$</td>
<td>16 days</td>
<td>exp. stream/Arizona</td>
<td>80</td>
</tr>
<tr>
<td><em>Leptohyphes packeri</em> (Ephemeroptera)</td>
<td>0.66$^a$</td>
<td>240</td>
<td>12 days</td>
<td>stream/Arizona</td>
<td>74</td>
</tr>
<tr>
<td><em>Polypedilum</em> spp. (Diptera)</td>
<td>0.71</td>
<td>258</td>
<td>7–12 days</td>
<td>stream/Georgia</td>
<td>9</td>
</tr>
</tbody>
</table>

$^a$ Estimated as annual P/B divided by 365.
$^b$ Estimated as ln(final mass/initial mass)/developmental period (days).
$^c$ Approximate annual P/B = daily growth rate × 365; provided as index only (assumes continuous development and exponential growth).
$^d$ Estimated as $^{ab}$ using length-frequency data and length-weight equations (10).
$^e$ Estimated as $^{cd}$ assuming initial length of 0.5 mm (cf. 63) and length-weight equations (10).
TABLE 2  Examples of exceptionally low and high levels of production for macroinvertebrate communities in streams and rivers. Values are standardized to dry mass (DM) equivalents (147).

<table>
<thead>
<tr>
<th>Location</th>
<th>Production (g DM • m$^{-2}$ • year$^{-1}$)</th>
<th>Annual P/B</th>
<th>Habitat—organisms</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Low Production</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>North Carolina</td>
<td>1.2</td>
<td>5.2</td>
<td>headwater stream with four-year detritus exclusion</td>
<td>143</td>
</tr>
<tr>
<td>Alaska</td>
<td>$\sim$ 0.8 to 2.2$^a$</td>
<td>$\sim$5.5</td>
<td>tundra stream (unfertilized reach)</td>
<td>57</td>
</tr>
<tr>
<td>South Carolina</td>
<td>2 to 4.1</td>
<td>7.5 to 9.4</td>
<td>stream—collector-gatherers, filter-feeders, predators</td>
<td>128</td>
</tr>
<tr>
<td>Norway</td>
<td>3.9</td>
<td>$\sim$ 4.8</td>
<td>river—high discharge upstream of a weir</td>
<td>41</td>
</tr>
<tr>
<td>Minnesota</td>
<td>5.4</td>
<td>4.2</td>
<td>river—collector-gatherers, predators, shredders</td>
<td>79</td>
</tr>
<tr>
<td><strong>High Production</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arizona</td>
<td>121 to 135</td>
<td>78 to 117.4$^b$</td>
<td>desert stream—midges, mayflies, collector-gatherers</td>
<td>39, 74</td>
</tr>
<tr>
<td>Germany</td>
<td>129</td>
<td>0.7</td>
<td>lake outflow—bivalves dominate biomass</td>
<td>109</td>
</tr>
<tr>
<td>North Carolina</td>
<td>169$^c$</td>
<td>8.5</td>
<td>river—primarily filter-feeding caddisflies</td>
<td>53</td>
</tr>
<tr>
<td>Georgia</td>
<td>200$^c$</td>
<td>8.2</td>
<td>river—primarily filter-feeding caddisflies</td>
<td>52</td>
</tr>
<tr>
<td>Wales (U.K.)</td>
<td>268</td>
<td>3.0</td>
<td>moat stream—Tubificidae (organic enrichment)</td>
<td>82</td>
</tr>
<tr>
<td>West Virginia</td>
<td>612$^c$</td>
<td>30.3</td>
<td>below dam—black flies and filter-feeding caddisflies</td>
<td>141</td>
</tr>
<tr>
<td>Iceland</td>
<td>$\sim$40 to 880</td>
<td>$\sim$2.5 to 11</td>
<td>lake outflow—black flies (eight-year study)</td>
<td>45</td>
</tr>
<tr>
<td>England</td>
<td>$\sim$1000</td>
<td>2.2 to 2.7</td>
<td>pond outflow—black flies (summer cohorts)</td>
<td>154</td>
</tr>
</tbody>
</table>

$^a$ Six-year range for three dominant invertebrate taxa.

$^b$ P/B based on zero winter biomass.

$^c$ Primarily bedrock substrata covered by the hydrophyte Podostemum ceratophyllum, which provides habitat structure.
The literature concerning freshwater macroinvertebrate life histories (25, 136, 145) and production (8, 147) is large. Rather than providing a global review of this information, we focus on how selected life-history attributes of different developmental stages of benthic insects [egg, first-instar larva (= “first-instar” hereafter), larva during subsequent instars (= “larva” hereafter), pupa, and adult] and other macroinvertebrates influence their production. We pay particular attention to factors that influence growth rate or biomass because these will have the strongest influence on secondary production. Although examples from both lentic and lotic habitats are included, we focus primarily on streams.

EGGS AND FIRST-INSTAR

Estimates of the biomass of adult insects emerging from streams are generally only about 24% of total annual production (130), and most estimates of adult mortality prior to oviposition exceed approximately 95% (36, 47, 74, 150). These high losses indicate that egg production will be a small fraction of annual production. The few attempts to measure egg production support this assessment (e.g. approximately .03 to 2% of annual production; 22, 99, 153). Although rarely considered in this context, this statistic is important because the egg and first-instar represent the initial investment of biomass that begins the process of production. Other factors directly related to the egg and first-instar that may have important influences on production are mortality, hatching synchrony, dispersal and cannibalism.

Mortality

The initial biomass of a cohort will be strongly influenced by egg mortality. Available information for stream insects indicates that hatching success is usually fairly high, often ranging from 70% to more than 90% (20, 36, 87, 104, 153, 157). Low levels of hatching success (approximately 20%) have also been reported (29). Agents contributing to egg mortality include invertebrate predators and parasitoids (36, 104, 106, 111, 145) and zoosporic fungi (87). Physical disturbances such as flooding can impose high levels of mortality for taxa that oviposit near the water’s surface (36), as well as eggs resting among substrata (46, but see 157).

Hatching Synchrony

Eggs of many aquatic insects show synchronized development and hatching (21, 85, 106, 153). Synchronization offers several advantages, including reduction of cannibalism (61, but see 153) and efficient access to food resources available only for a short period (e.g. autumn detritus) (85). Asynchronous egg development, however, is also widespread among aquatic insects (35, 55, 92, 106), and may have an important role in recolonization of streams following scouring floods (157). The pros and cons of hatching synchrony in the context of secondary
production have received little attention. Given similar larval abundances of the mosquito *Aedes triseriatus*, cohorts with synchronous development yielded smaller adult females compared with cohorts with asynchronous development (33). The diverse size-structure of larvae in the asynchronous cohorts apparently reduced competition and enhanced larval growth and production (33).

**First-Instar**

The primary function of the first-instar of many aquatic insects is dispersal, which is distinct from subsequent instars whose function is primarily growth (104, 106). A dispersal stage shortly after hatching is critical for stream insects where access to oviposition sites may not allow optimal placement of eggs (42, 104, 106). Competition near oviposition sites due to clumped distribution of eggs may lead to reduced feeding rates, dispersal, and density-dependent mortality (42, 104). Mortality of first-instar can be high. Willis & Hendricks (153) reported 93% mortality for first-instars of the caddisfly *Hydropsyche slossonae*.

Cannibalism by first-instars has been documented for the Odonata and Trichoptera (61, 104, 153). Willis & Hendricks (153) reported that 10% to 20% of first-instars of *H. slossonae* cannibalize siblings, a statistic that is remarkably similar to their survivorship (approximately 10%). Cannibalism may have important implications for growth and survival of larvae. By eating siblings, first-instars of some insects can double their survival probabilities and proceed to the second instar (153).

**LARVA**

The egg and first-instar represent the initial investment of biomass for subsequent production, but factors influencing individual growth rates and biomass accrual of larvae following these initial stages are probably the most critical in determining overall secondary production by stream insects. In this section we focus on the extremes of variation in growth (slow versus fast) and biomass (low versus high) of freshwater benthic macroinvertebrates, and show how these interact to determine extreme levels of production (low versus high) by populations and communities.

**Slow Growth Rates and Long Life Cycles**

To our knowledge, larvae of the xylophagous elmid beetle *Lara avara* have the slowest growth rates (∼0.3% to 0.4% day⁻¹) and the longest life cycles (5–6 years) of all stream insects (131; Table 1). The slowest growth rates recorded among all aquatic insects (∼0.1% day⁻¹; Table 1), however, are those for larvae of *Chironomus* inhabiting tundra pools in northern Alaska. These larvae require seven years to complete their life cycle (23, 24). Other reports of extremely slow growth rates (<1% day⁻¹) and long life cycles (∼2+ years) for stream insects are summarized in Table 1. Although the majority of these are for species from
cool-temperate streams, long life cycles are not restricted to higher latitudes. Sweeney et al (137) studied the tropical mayfly *Euthyplocia hecuba* in Costa Rica and found growth rates of $<1.4\%$ day$^{-1}$ and a life cycle of 22 months (Table 1). This is the first evidence of a life cycle of more than one year for a tropical mayfly.

Crayfish (Decapoda), particularly those from streams at high latitudes or altitudes, exhibit some of the lowest growth rates and longest life cycles reported for stream macroinvertebrates (Table 1). Examples of low annual P/Bs for crayfish include: 0.3 to 0.4 (18, 151); 0.58 to less than 1.0 (70, 91); or approximately 1.0 (132). Life cycles of more than 10 years have been reported for several species (6, 18, 70, 151).

Without doubt, the slowest-growing and longest-lived stream macroinvertebrates are mollusks (Table 1). The freshwater mussel *Unio*, for example, has annual P/Bs of less than 0.1 and life cycles greater than 10 years in England and Europe (94, 108; Table 1). Although not measured, the P/Bs of the mussel *Margaritifera* are probably even lower because some populations in North American streams have modal ages ranging from 48 to 100 years (134, 140). In contrast, some bivalves such as the Asiatic clam *Corbicula fluminea* and the zebra mussel *Dreissena polymorpha* have higher growth rates and shorter life cycles (three years). Populations of *Corbicula* have annual P/Bs ranging from 0.5 to 1.8 (133), and P/Bs for zebra mussels range from 3.3 to 3.5 (76). Other mollusks that have slow growth rates include the pleurocerid snail *Elimia*, with annual P/Bs ranging from about 0.5 to 1.5 and life cycles of two to three or more years for eight populations in Alabama (66).

Rapid Growth Rates and Short Life Cycles

The highest annual P/B measured for a stream insect is 258 for larvae of the chironomid *Polypedilum* in the Ogeechee River in Georgia (9; Table 1). The bioenergetic significance of this statistic becomes clear if one realizes that it equals a daily P/B of 0.7, indicating that this population replaces its biomass almost daily. This growth rate is among the highest estimated for metazoans, and is more similar to growth rates of microbes than to other stream macroinvertebrates. Relatively rapid growth for other macroinvertebrates, particularly the Ephemeroptera, have also been reported for this system (e.g. annual P/Bs $\sim$60 to 90; 12). Warm temperatures (maximum $\sim$31 to 33$^\circ$ C), a large supply of high-quality food, and small body size contribute to rapid growth rates of mayflies and midges in the Ogeechee River (9), as well as other warm-temperate streams (e.g. 39, 46, 51). However, the effect of such factors is not universal.

Jackson & Sweeney (75) documented growth rates and developmental time for 35 species of Ephemeroptera, Plecoptera, Trichoptera, and Chironomidae in Costa Rican streams (annual range of water temperature = 20–23$^\circ$ C), and showed most taxa had multivoltine life cycles (32 of 35 taxa), overlapping cohorts and complex size structure. The results from this study were surprising, however:
Although food and temperature were apparently not limiting, the highest growth rates measured for insects in these tropical streams (~0.29 day⁻¹ for Polypedilum epomis; Table 1) were well below those reported from some warm-temperate streams (e.g. ~0.66 day⁻¹ for Leptohyphes packeri; 0.71 day⁻¹ for Polypedilum spp; Table 1).

Rapid growth rates and short developmental times are not limited to macroinvertebrates of tropical or warm-temperate streams. A short life cycle (approximately 16 days) and extremely rapid growth rates (~0.56 day⁻¹; Table 1) have been reported for the midge Orthocladius calvus in an outdoor recirculating stream in England (80). A short life cycle of 35 to 45 days and a relatively high growth rate (~0.17 day⁻¹; Table 1) was also reported for the midge Diamesa incallida in a spring stream in Germany (96). These rapid growth rates are particularly surprising given the large terminal size of the larvae of these taxa—9 to 10 mm in length, 0.7 to 0.8 mg dry mass (= DM) —and relatively cool temperatures of their habitats (10.5° C-80; 8° C-96). Nevertheless, comprehensive studies of the growth rates for midges in many cool-temperate streams indicate that these are generally less than approximately 0.05 day⁻¹ (17, 63).

Factors Controlling Growth Rates

The maximum and minimum limits for growth rates of freshwater macroinvertebrates are determined by food quality (9, 49, 51, 71, 93, 131), temperature (9, 39, 44, 49, 71, 75, 93), time available for development (24), body size (9, 70, 75, 113, 137, 151), population density (37, 56, 66) and intrinsic genetically based constraints (140). These major factors have been the subject of comprehensive reviews (cf. 30, 81, 136, 140; see also 49). Rather than focusing on these here, we will address the effects of several additional factors that, although probably significant, are generally not considered in the context of production.

Region and Habitat Template  The highest growth rates known for any stream insect are reported for the warm-temperate streams, Sycamore Creek and the Ogeechee River (9, 12, 46, 74). The organisms involved (primarily midges and mayflies) not only grow rapidly, but also complete life cycles rapidly because they attain relatively small sizes (e.g. length 4 to 5 mm; 9, 12, 46). Given the habitat template offered by Sycamore Creek and the Ogeechee River, one explanation for the extremely high growth rates may lie in the balance of fitness costs associated with fast growth and short life cycles versus slow growth and long life cycles (97). In habitats where risk of mortality is high during development, growth rate should be maximized and size minimized; where risk of mortality is low, size should be maximized, generally resulting in slower growth rates and longer developmental periods (75).

In Sycamore Creek, mortality due to random flash flooding (see “Larval Production”), and in the Ogeechee River, mortality from dehydration because of frequent stranding of snag communities, has apparently resulted in selection for
taxa with rapid growth rates and short life cycles (12, 13, 46, 74). The extreme rates of growth and turnover recorded for these systems are attributable to warm temperatures, abundant food and a harsh disturbance regime. Attributing extremely high growth rates and production to these factors may seem counter-intuitive, but given a similar thermal regime and food supply, with a more benign disturbance regime, selection for taxa with longer life cycles and a larger terminal size may result in lower average growth rates and production (see "Larval Production"; 75).

**Body Size and Armor**  Although large body size is often associated with high fecundity (117), a period of prolonged growth may be required with increased risk of mortality. Perhaps in response, many taxa with extremely slow growth rates (bivalves, snails, crayfish) tend to be large and armored compared with those with rapid growth rates (cf. Table 1). Protection from predation (94, 113, 116) or physical disturbance (140) may allow these groups to reduce mortality and accrue biomass over longer life cycles than most insects (also see 19). Larvae of the exceptionally slow-growing elmid beetle *Lara* provide an important example from the insects (Table 1). These larvae presumably avoid predation by possessing remarkably heavily sclerotized bodies and by remaining concealed within feeding grooves on submerged wood (131).

**Presence of Predators**  The mere presence of a predator within a stream community may have a profound influence on growth rates of prey (27). When exposed to predators, or chemicals released by predators or injured conspecifics, benthic insects typically show reduced movement activity, sheltering behavior (121), or greater nocturnal activity compared to daytime activity (89). Such behaviors reduce time spent feeding, which reduces growth rates (90). Peckarsky et al (103), for example, showed that larvae of the mayfly *Baetis bicaudatus* did not grow in the presence of predators, but in the absence of predators larval mass increased 50 percent during one week. Similarly, data from field observations and experiments predicted that in the presence of predaceous stoneflies and trout, *B. bicaudatus* emerge at a mass 50% smaller compared to larvae reared in the absence of predators (90). However, growth rates do not always decrease in the presence of a predator. The pulmonate snail *Physella* shows higher growth rates and attains a larger size in the presence of their crayfish predators in Oklahoma streams (27).

Few data show how growth rates differ among macroinvertebrate communities subject to different levels of predation, but available examples indicate that predation may have a significant effect. Huryn (65) studied production of macroinvertebrate communities in two streams with high and low levels of predation by fish (i.e. approximately 100% versus 18% of macroinvertebrate production consumed). The community subjected to high predation was characterized by individuals of smaller size and higher growth rates (annual P/B = 6.9) compared to that experiencing low predation (annual P/B = 3.9) (65). Body size is often
negatively correlated with growth rate (e.g. 4, 75), so higher growth rates observed in this study (65) may be either an indirect effect of size-selective predation, or a bias toward rapidly growing taxa that attained smaller body size, or both.

**Competition** Competition can affect growth rates of macroinvertebrates in streams, particularly grazers (56, 37). A tenfold increase in the density of the grazing caddisfly *Glossosoma nigrior* reduced prepupal biomass by approximately 25% (56). High abundance of larvae of the grazing caddisfly *Helicopsyche borealis* following dry winters in a California stream resulted in lower pupal mass (approximately 25% lower) compared to years with wet winters (37). Scouring flows during wet winters reduced both larval abundance and competition for food (37). Growth rates of the pleurocerid snail *Elimia* in six Alabama streams also showed a strong negative relationship with population biomass, suggesting that growth was limited by competition for periphyton (66).

**LARVAL PRODUCTION**

Production is the product of growth rate and biomass (8). The highest levels of secondary production will therefore occur when growth rates are rapid and biomass is high (8). However, because these factors are often negatively correlated, both parameters are rarely maximized simultaneously (37, 56, 66; see "Competition"). Consequently, high levels of production observed in the field usually result from rapid growth rates plus low biomass, or slow to moderate growth rates plus high biomass. To illustrate the fundamental importance of this simple observation, we provide examples using chironomid production in two North American streams.

**Sycamore Creek, Arizona—A Dynamic System** Sycamore Creek is a warm temperate, desert stream with annual water temperatures ranging from 5 to 33° C. Sycamore Creek is subject to two to nine flash floods each year that scour substrata and reduce benthic insect abundance by as much as 98% (46). Annual production of Chironomidae is ~58 g dry mass (= DM) m⁻² of stream bottom (74). Average biomass is relatively low (~0.5 g DM m⁻²), but larval growth rates are rapid (~ 0.3 day⁻¹), larvae are small (maximum length <5 mm), and development is continuous with approximately 20 or more generations per year (Figure 1). These factors result in an annual P/B of 121.5.

**Juday Creek, Indiana—An Inertial System** Juday Creek is a temperate forest stream with annual water temperature ranging from 2.5 to 17° C. Floods are infrequent and seasonal. Annual production of Chironomidae is 29.7 g DM m⁻² (16). Although biomass is high compared to Sycamore Creek (~4.6 g DM m⁻²), larval growth rates are slower (maximum <0.09 day⁻¹), larvae of the dominant taxa are larger (~7 to 11 mm), and only two to three generations are completed
Figure 1  Life cycles of midge larvae in a warm-temperate desert stream prone to random flash flooding (Sycamore Creek), and a cool-temperate stream with more stable flows (Juday Creek). Emergence and oviposition occur at the maximum length indicated by growth trajectories. Left: Generalized life cycle for midge assemblage of Sycamore Creek (46, 74). Breaks indicate the effects of random flash floods (cf. 46). Right: Life cycles for Diamesa nivoriunda (black) and Cricotopus bicinctus (gray). Both taxa are major contributors to midge production in Juday Creek (16, 17).

each year (Figure 1). These factors result in an annual P/B of 6.7.

The comparison of these studies shows that the life history attributes of midges in Sycamore Creek resulted in dynamic control of production, whereas those in Juday Creek resulted in inertial control. In Sycamore Creek, rapid growth rates, short life cycles, and small terminal size of larvae compensated for low biomass and resulted in high production and P/Bs (see “Region and Habitat Template”). In Juday Creek, midges had longer life cycles, slower growth, and larger terminal sizes, yet chironomid production in Juday Creek was similar to that of Sycamore Creek because biomass was approximately nine times higher in this cool-temperate stream. The distinction between dynamic and inertial control of production is particularly evident in these examples. The balance between growth rate and biomass in determining macroinvertebrate production in most highly-productive streams appears to be biased toward inertial control (Table 2).

Extremes of Larval Production

High Production  The highest production known for an aquatic insect is 7.4 and 8.8 g carbon m$^{-2}$ day$^{-1}$ for each of two summer cohorts of filter-feeding larvae of the black fly S. noellleri in a lake outlet stream (154, Table 2). Minimum annual production was 414.6 g carbon m$^{-2}$; total annual production probably exceeded 500 g carbon m$^{-2}$ (~1 kg ash-free dry mass (= AFDM) m$^{-2}$; cf. 88). This example is extreme, however. More reasonable “extremely high” rates of community-level production range from 100 to 300 g DM m$^{-2}$ year$^{-1}$ (8; Table 2)
What factors contribute to high secondary productivity? Estimates of annual production >100 g DM m$^{-2}$ are usually for filter-feeding insects. Examples include hydropsychid caddisflies (15, 52, 53, 101, 141; Table 2) and black flies (14, 45, 154; Table 2). Some filter-feeding mollusks also show high levels of production (e.g. 26, 109; Table 2). High production by filter-feeders is always due in part to relatively rapid growth rates and high population biomass (e.g. some black flies; Table 2) or to slow to moderate growth rates combined with exceptionally high biomass (e.g. bivalves, hydropsychids, some black flies; Table 2). The astonishingly high production of filter feeders in some lake outlet streams (Table 2) is subsidized by favorable thermal regimes and nutrient-rich plankton exported from the lake, which enhance growth rates and allow for accrual of high levels of population biomass (155; see “Biomass Accrual”). Levels of annual production approaching 100 g DM m$^{-2}$ are also reported for communities of collector-gathering macroinvertebrates in warm-temperate streams with abundant food and a harsh disturbance regime (e.g. 9, 40, 74; see “Region and Habitat Template”).

**Low Production**

Estimates of macroinvertebrate production >100 g DM m$^{-2}$ are exceptionally high. But what level of production should be considered exceptionally low? Based on a summary of 58 studies of production for entire macroinvertebrate communities, 40% reported levels of less than 10 g DM m$^{-2}$ year$^{-1}$, and 78% reported levels of less than 50 g DM m$^{-2}$ year$^{-1}$ (8). Only three studies, however, reported levels less than approximately 3 g DM m$^{-2}$ year$^{-1}$. Data available since Benke’s (8) review are in accordance with these values (e.g. 64, 65, 109, 142, 143; Table 2).

What factors contribute to low secondary productivity? Obviously, any factor that reduces growth rates or biomass of macroinvertebrates will also reduce their production. Low food quality and quantity, and low temperature can reduce growth rates (see “Factors Controlling Growth Rates”). Reductions in biomass can be caused by many factors, including emigration (60, 67), predation and competition (78, 149), food availability and nutrients (57, 79, 105, 143), disturbance (40, 41, 57, 66, 122, 123), availability of suitable substrata (14, 28, 52, 53, 109, 128), and dissolved oxygen and low stream velocities (128). Several studies suggest that bottom-up control (food limitation) has a critical influence on the production of stream macroinvertebrates. For example, one of the lowest levels of secondary production measured in a stream resulted from a four-year experimental exclusion of terrestrial detritus inputs to a heavily shaded headwater stream in North Carolina (142, 143; Table 2). Exclusion of detritus resulted in a consecutive four-year decline in abundance (−77%), biomass (−79%), and secondary production (−78%) of both primary and secondary consumers in the dominant habitat, which underscores the importance of bottom-up control of productivity (143). Likewise, the addition of nutrients to an arctic tundra stream increased both primary and secondary productivity (105).
STREAM INSECT PRODUCTION

FATE OF LARVAL PRODUCTION

Biomass Accrual

Biomass of stream macroinvertebrates accrues whenever gains due to production or immigration exceed losses within a given area (see “Emigration/Immigration”). Accumulating biomass may have simultaneous positive and negative influences on rates of production because of its dual role as both an investment that contributes to future production and a burden because of the greater fraction of available energy needed for its maintenance (19, 66; see “Disturbance”). A survey of 57 studies that estimated biomass for entire macroinvertebrate communities revealed that 68% were less than 5 g DM m\(^{-2}\) and 81% were less than 10 g DM m\(^{-2}\) (8). Levels of biomass for entire macroinvertebrate communities in streams appear to be generally less than 5 to 10 g AFDM m\(^{-2}\). Estimates approaching 100 g m\(^{-2}\) are rare (8, 52, 53, 109).

High levels of biomass accrual often characterize taxa with long life cycles (e.g. more than two years) and overlapping cohorts. In such cases, high biomass can offset relatively low growth rates and result in surprisingly high production (e.g. 23, 151). The annual P/Bs of populations that tend to accrue biomass over successive cohorts are usually less than one (e.g. 23, 24, 66, 94, 151).

Long life cycles are not required for substantial accrual of biomass, however. Populations of filter-feeding macroinvertebrates, most with life cycles of less than one year, attain exceptionally high levels of population biomass. Biomass of filter-feeding larvae of the black fly S. noelleri in a lake outlet stream in England, for example, can exceed 80 g carbon m\(^{-2}\) (~160 g AFDM m\(^{-2}\); cf. 88) (154; Table 2). This extraordinary biomass accrues in a matter of weeks and is due to larval densities that may exceed one million individuals m\(^{-2}\). Animal populations that maintain such high levels of biomass require a continuous and reliable source of energy. This demand is met by filter feeders in stream habitats with stable substrate, adequate current velocity, and high organic seston concentrations, where they are able to exploit the kinetic energy of flowing water for the delivery of food produced elsewhere (28). Because of these subsidies, filter feeders expend less energy in search of food while supporting high levels of biomass (28, 154; Table 2). For most communities of stream insects, biomass losses are relatively high compared with biomass accrual, as indicated by annual P/Bs that are often more than five and may exceed 100 for some communities (8).

Biomass Loss

**Molting and Silk Production** Loss of biomass as cast exuviae by stream macroinvertebrates has received little study with regard to its effects on production, although this may be substantial (5). Molting losses for several species of Ephemeroptera and Plecoptera range from 8% to 21% of larval AFDM (see 5),
and losses by crayfish can range from 21% to 38% of AFDM at each molt (70). Molting losses for the dobsonfly *Corydalus cornutus* are approximately 10% (22). Molting losses for most other holometabolous insects are expected to be lower, e.g. 2% to 4% for Trichoptera (5, 72, 99). Lower losses for larvae of the Holometabola are expected to be a function of lower proportional losses of biomass at each molt (5, 22, 72, 99) and lower molting frequency (58, 72, but see 22).

Molting losses may have additional consequences for production because of the compounding effect of exponential growth. For example, assuming that a mayfly larva grows at 5% day$^{-1}$ over 150 days, molts 14 times during 15 stadia, and loses 12% of its mass at each molt (cf. selected Plecoptera, Ephemeroptera), its final mass will be 2.5 mg. Given an identical growth rate and period, a caddisfly larva that molts 4 times during 5 stadia and loses 5% of its mass during each molt (cf. selected Trichoptera) will achieve a final mass of 12.3 mg. In the case of the mayfly, approximately 0.7 mg (about 28% of production) of individual biomass will be discarded as exuviae, compared with 0.4 mg (approximately 3% of production) for the caddisfly. Although the mass lost as exuviae is only about two times greater for the mayfly, its final body mass (= individual production) is approximately five times lower than the caddisfly.

The bioenergetic efficiency of biomass accrual by most Holometabola is predicted to exceed that of most Hemimetabola. However, the lack of a hardened exoskeleton in many holometabolous taxa may require substantial expenditure of silk for construction of retreats and protective cases (e.g. Chironomidae, Trichoptera). Silk used in case construction by Trichoptera, for example, requires 12% to 23% of annual production (69, 72). Other similar losses include production of silk for holdfasts by black fly larvae, production of mucus by gastropods (marine example 31), and production of glochidia by mussels (94).

The fate of molted exoskeletons, silk, or mucus produced by stream macroinvertebrates has received little attention. However, in some ecosystems it has been suggested that these are a major flux of carbon. Molted exoskeletons from krill in the Antarctic Ocean may be one of the major sinks of carbon in Antarctic waters (95). Although large numbers of molted exoskeletons are routinely found in drift samples from streams (59, 135), the bioenergetic consequences and fate of these are unknown. Silk produced by hydropsychid caddisflies can function as a substrate for calcium carbonate precipitation, increases travertine deposition rates in hardwater streams (32), and may indirectly affect community structure by adhering and stabilizing sediment particles (B Statzner, personal communication).

**Disturbance** Many studies have examined the effects of physical disturbance on macroinvertebrate abundance. However, the effects of disturbance on their biomass has received surprisingly little attention, although available information indicates that physical disturbance may have a major effect on production dynam-
ics of stream communities. Five to 50-fold reductions in biomass were measured following floods in an unstable, braided New Zealand stream (122, 123), and flash floods reduced macroinvertebrate biomass by as much as 98% in Sycamore Creek (40, 51). Accrual of biomass following disturbance is rapid in both of these systems, with recovery to pre-disturbance levels occurring in less than three months (40, 51, 122). Streams with low levels of disturbance often have higher biomass than more frequently disturbed streams (112, 114, 115). Channel structures serving as refugia for freshwater mussels provide an excellent example of the potential effect of disturbance on biomass accrual by long-lived macroinvertebrates (139). Beds of the freshwater mussel *Margaritifera* with the largest and oldest populations (modal age ~46 to 100 year) occur in large block-boulder reaches, and it has been hypothesized that such large, relatively immobile substrata protect *Margaritifera* from being buried during 50- to 100-year floods (139).

Removal of biomass by disturbance may affect growth rates via density-dependent competition for food. This effect on growth rate complicates predictions of how disturbance may affect production. Some studies have indicated that a reduction in biomass as a result of disturbance may result in higher growth rates (37, 66). But higher growth rates may not necessarily lead to increased production, compared to pre-disturbance levels, if losses of biomass are severe and frequent relative to the developmental periods of the dominant producers (66). In Sycamore Creek macroinvertebrate biomass tends to decline following extended periods without disturbance (e.g. more than 60 to 80 days) because of reduced food quality resulting from cyclical coprophagy (51). Disturbance may thus actually facilitate high food quality and consequently high levels of insect production in this warm-temperate desert stream (40, 51, 74).

**Emigration/Immigration** Simultaneous losses and additions of macroinvertebrate biomass occur continuously via immigration and emigration of individuals among stream habitats and reaches. Most movements are probably in the form of drifting individuals, although upstream movements are of considerable significance in some geographic regions, particularly those by snails and atyid shrimp (67, 110, 119). The effect of such migrants as a net gain or loss of biomass has received little study. Their effects may be significant, however, especially when interpreting results of studies where the spatial scale of observation is limited (e.g. single habitats; 54). Large larvae of the mayfly *Tricorythodes atratus* in Minnesota, for example, drift from riffles and accumulate in pools, while small larvae remain in riffles (54). This behavior will result in erroneously high (pools) or low (riffles) estimates of production if only one habitat is considered (54). Movements of stream invertebrates into ephemeral floodplain habitats have been regularly documented, but the effects of such movements on community or ecosystem-level processes are rarely quantified (see 68). In one case, migrations from stream channels to forested floodplain wetlands in Virginia resulted in a small input of biomass to the floodplain (less than four percent of the annual mean biomass and
less than one percent of the annual invertebrate production on the floodplain, 127).

To our knowledge, quantitative estimates of movements of macroinvertebrate biomass between stream reaches are not available. However, these movements probably have significant effects on reach-level patterns of production. Hinterleitner-Anderson et al (60), for example, showed that fewer larvae of the mayfly *Baetis* drifted from a fertilized reach of an Alaskan river when compared with those drifting from an unfertilized reach. Larvae drifted from the unfertilized (low food resource) reach where per-capita food supply was limiting growth, and accumulated in the fertilized (high food resource) reach downstream (60). This study provides some support for the long-standing hypothesis that drift may represent “excess production” where animals migrate out of stream reaches as a function of resource availability (cf. 2, 146).

Predators may also have important influences on the biomass distribution of macroinvertebrates in streams (125). The mere presence of predatory macroinvertebrates tends to increase behavioral drift of prey, thereby increasing emigration of individuals from patches with predators and immigration into predator-free areas (125). The presence of invertivorous fishes, on the other hand, may result in a reduction in the behavioral drift of macroinvertebrates which should decrease rates of emigration (43). Although the occurrence of such movements within stream channels is well documented (43, 125), their effects on spatial and temporal patterns of macroinvertebrate biomass and production remain unstudied.

**Predation and the Allen Paradox** The fate of most production by stream macroinvertebrates may be to support production by their predators. High demands on macroinvertebrate production by vertebrate predators have been reported for approximately 50 years (i.e. “Allen Paradox” 1, review in 149). Most recently, Huryn (65) used a comprehensive production budget to show that brown trout (*Salmo trutta*) consumed virtually all macroinvertebrate production in a New Zealand stream (approximately 101% to 110%). Similar rates of prey consumption by salmonids were reported for 11 of 13 streams for which information is available (64, review in 149).

The Allen paradox is not restricted to fish-macroinvertebrate interactions. Predaceous invertebrates in a sand-bottomed stream in Virginia consumed 94% of prey production (126). This estimate did not account for production by prey in the hyporheic zone of the stream, and their inclusion indicated that predator demand was still substantial (66% of prey production; 126). In another study, predaceous invertebrates and larval salamanders consumed an estimated 74% to 83% of macroinvertebrate prey production in two fishless mountain streams in North Carolina (83). Wallace et al (142) measured production by macroinvertebrate predators and prey in one of these same streams for eight years and showed that predator production required essentially all prey production (approximately 100%), and that predator production is probably limited by prey production. These studies together indicate that the effects of predation may result in vanish-
ingly small surpluses of prey production (see “Adult Emergence as a Function of Larval Production”).

Although a number of studies provide compelling evidence that predation can be an important sink for production by stream macroinvertebrates (64, 83, 126, 142, 149), such findings are by no means universal (e.g. 65). Under conditions where predator populations are limited by nontrophic factors (e.g. spawning habitat, floods), or in cases where prey are relatively immune to predation (e.g. mussels; 94), consumption of production by predators may be low. The fate of surplus macroinvertebrate production in such systems is unknown, but probably includes losses due to disturbance (see “Disturbances”), emigration (see “Emigration/Immigration”), disease (29, 78), parasitism (138), and emergence (see Section, “Adult Emergence as a Function of Larval Production”).

PUPA

The role of the pupal stage in production dynamics of holometabolous stream insects has received little attention. As a nonfeeding stage, the pupa functions as a biomass sink rather than a source of biomass production. Losses of pupal mass occur through respiration, molting, and mortality.

Pupal Respiration and Molting

Metabolic processes of insect pupae rely on energy and nutrients accumulated as larvae. Studies of the terrestrial sphinx moth *Manduca sexta* and darkling beetle *Tenebrio molitor* indicate that losses of wet mass may range from 14% to 50% (98). There are few similar studies for aquatic insects, but the available examples indicate similar losses, including an approximate loss of 19% to 21% (DM) during prepupal to pupal transformation for the caddisfly *Glossosoma nigrior* (56), and an approximate loss of 48% loss (J) during prepupal to adult transformation for females of the dobsonfly *Corydalus cornutus* (22).

Pupal Mortality

The limited data available indicate that mortality of pupae can be substantial. Total adult emergence for a population of the caddisfly *Potamophylax cingulatus* in a Swedish stream accounted for only about ten percent of total pupal biomass (99). Mortality rates of more than 45% were observed for hydropsychid caddisfly pupae in an Ontario stream (118), and Willis & Hendricks (153) showed that pupae of *Hydropsyche slossonae* in a Virginia stream had the second highest mortality rate (76%) of all aquatic life-history stages except the first-instar. Predaceous chironomid larvae have been regularly implicated as agents of high levels of pupal mortality for hydropsychid caddisflies (102, 118, 153). Larvae of the Empididae (Hemerodromiinae) are also known to be predators of caddisfly pupae in South America (77). Substantial pupal mortality may also result from desiccation due to stranding. Stranding apparently resulted in the death of 38% of
prepupae of the caddisfly *Neophylax fuscus* in an Ontario stream (86). Mortality directly associated with adult emergence may also be high. Rutherford (118), for example, reported that 34% of pharate adult hydropsychid caddisflies ("swimmers") drowned before molting to the adult stage.

**ADULT**

The aerial adults of stream insects form links between stream and riparian food webs, and the mortality associated with this process represents the endpoint for much adult production. In most studies, however, the hatching of eggs and emergence of adult insects are often viewed as starting points and endpoints of their life cycles. Because of this limited perspective, little is actually known about quantitative processes that affect the adult stage of stream insects.

**Adult Emergence as a Function of Larval Production**

A review of data for 18 populations of stream bisects in Europe and North America indicated that emerging adult biomass consistently represented approximately 24% of annual production (130). This finding is remarkably similar to the proportion of annual insect production emerging as adult biomass from a warm-temperate desert stream (24% to 29% Diptera, 27% Trichoptera, 2% to 15% Ephemeroptera, mean ~19%; 74). This similarity is particularly striking because annual production reported by Jackson & Fisher (74) and for the stream populations included in the analysis by Statzner & Resh (130) ranged over three orders of magnitude (<1 to >100 g DM m\(^{-2}\)).

**Fate of Adult Biomass**

**Adult Growth** Tissue growth by adult stream insects, which occurs for selected Odonata, Plecoptera, Coleoptera, Trichoptera, and Diptera, has not been addressed in studies of secondary production. With the exception of black flies, adult growth has been perhaps best documented for the Odonata and Plecoptera. As predators, adult Odonata may increase their mass by 84% to 125% (3, 84). Adult females of the stoneflies *Leuctra* may gain 50% and *Siphonoperla* may gain 25% of their emergence weight through terrestrial feeding (156). Adult males of nemourid stoneflies may double their mass and mature females may gain up to three times the mass of freshly emerged females by feeding on lichens, algae, and pollen (5). Although unstudied, production by aerial adults may provide a further subsidy to riparian food webs that is ultimately dependent on the benthic community in the adjacent stream.

**Adult Mortality** Mass-balance approaches show that the amount of adult insect biomass returning to streams to oviposit following emergence may be only a small fraction of that emerging from the stream. Jackson & Fisher (74) estimated that
of 23.1 g DM m⁻² of insects emerging from Sycamore Creek each year, only three percent returned to the stream. In a similar study, Gray (47) estimated that of 20 mg DM m⁻² of insects emerging daily from a prairie stream in Kansas, only one percent returned to the stream. Similar levels of loss have been shown for adults of insects emerging from forested streams, although biomass lost must be inferred from abundance. The abundance of females of the mayfly *Baetis* and the caddisfly *Apatania fimbriata* emerging from a forested German stream, for example, were compared with the abundance of egg masses to estimate approximately 90% to 99% and 82% mortality, respectively (36, 150). Based on the cited studies, it is apparent that most (e.g. > 80%) of the production of emerging adult stream insects, which may represent approximately 20% to 25% of total annual production, is supplied to riparian food webs.

**Sources of Adult Mortality** Wind, rain, extreme temperatures, and humidity have all been implicated as a source of mortality for aerial adults of aquatic insects (50, 73, 150). However, predation by insectivorous birds and bats is probably most significant. Fisher (38) estimated that a single flycatcher inhabiting the riparian zone of Sycamore Creek during the summer will consume all insect biomass emerging from 1000 m² of stream bed, or the total annual secondary production from 200 m² of stream bed. Gray (48) estimated that insectivorous birds inhabiting the riparian zone of a prairie stream in Kansas consumed 57% to 87% of emerging aquatic insects on a daily basis. Although these studies should be considered preliminary estimates, they provide some explanation for observations that only a small percentage of adult insects return to oviposit in the streams from which they emerge (36, 47, 74, 150). Terrestrial invertebrate predators, particularly spiders, ants, and ground beetles, are also sources of mortality for emerging aquatic insects (e.g. 50, 59, 150). However, their quantitative effects seem to be insignificant compared with those of vertebrate predators (cf. 38, 48, 152).

**SUMMARY AND CONCLUSIONS**

The annual production of stream macroinvertebrate communities worldwide ranges over four orders of magnitude (~10⁰ to 10³ g DM m⁻²). Factors contributing to high levels of production appear to be closely related to mode of feeding and life-history attributes of communities in temperate streams. Highly productive communities tend to occur in warm- to cool-temperate streams and tend to be dominated by filter-feeding bivalves, black flies, or caddisflies. Populations of filter-feeders are able to accrue and support high levels of biomass, which drives the very highest levels of production. Communities in warm-temperate streams subject to frequent disturbance also tend to be unusually productive. A harsh disturbance regime combined with a warm thermal regime apparently selects for taxa with short developmental times because of rapid growth rates and small terminal size. Because such life-history attributes tend to result in low biomass
accrual, high levels of production are driven by rapid growth rates rather than high levels of biomass. The very lowest levels of production, reported for macroinvertebrate communities in cool-temperate to arctic streams, appear to be attributable to a combination of seasonally low temperatures and nutrient or food limitation rather than specific modes of feeding or life-history attributes.

Most studies of the production biology of stream macroinvertebrates have focused on larval production as driven by growth rate and population biomass. In comparison, the relationship between production and attributes of the egg, first-instar, pupa, and adult stages are essentially unknown. As beginning and endpoints of the insect life cycle, it has been suggested that adult mortality may be an important bottleneck for larval production. The few comprehensive studies of the adult stage of stream insects do indicate that mortality before oviposition may be extremely high. Recent models based on stream insects, however, suggest that recruitment above surprisingly low thresholds may actually have little effect on larval production. Strong density-dependent control of abundance is predicted to result in continuous downstream movement of larvae in many stream systems (2, 146). Because production, rather than abundance per se, most directly underlies density-dependent competition for trophic resources, rates of larval production, rather than rates of oviposition by adults, may be the ultimate determinant of larval abundance and distribution for some populations of stream insects. The relationship between larval production and attributes of other life-history stages, both aquatic and terrestrial, deserves further study.

Most studies of benthic macroinvertebrate production either simply report levels of production for selected taxa, emphasize the effects of abiotic factors on production (i.e. habitat, temperature, water chemistry), or estimate the trophic support required to sustain selected taxa. Consequently, the role of food-web interactions in regulating production and its fate is poorly understood. For the few streams for which comprehensive production budgets are available, it is apparent that the fate of most macroinvertebrate production may be to support further production by predators. Extremely high losses to predators (~90% + in some cases) indicate that predation influences production of prey most significantly by removing biomass. However, the effects predators have on growth rates of prey may be as significant as the direct consumption of prey biomass is in determining community production dynamics. The mere presence of a predator within a stream community may influence the feeding behavior of their prey to the degree that an overall decrease in growth rates, and consequently community production, results (but see 27). By removing biomass while simultaneously affecting the growth rates of their prey, predators may have effects on the production of benthic communities that are much greater than currently recognized. Although potentially of great significance, such relationships remain largely unstudied in this context.

Current understanding of factors underlying differences in production among stream macroinvertebrate communities is hampered by the strong geographical bias of the few comprehensive studies, and by the dominance of studies concen-
trating on the effect of physical rather than biotic factors. Coordinated studies incorporating multiple streams with contrasting disturbance and nutrient regimes in diverse geographic regions are sorely needed for a predictive understanding of the relationship between the habitat template, life history, and secondary production.

Production is an interactive process that has simultaneous effects on multiple trophic levels—the potential for strong biotic control of production clearly exists. However, this potential has been ignored in most studies. Perhaps the major challenge for future studies of stream productivity will be to gain a predictive understanding of the role of biotic interactions (i.e. emigration/immigration, anti-predator behavior, and food-web interaction strength) in controlling quantities of materials and energy flowing through food webs.

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