major changes in jaw structure. Subsequent morphological innovations (e.g., elongate. more movable quadrate and su-

1980. Epilithic grazers were picked from rocks in each quadrat. with a 230 µm mesh drift net d~~~~~~~~~~ ~~ ~~~~~ ~~~

Research

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Seasonal Production Dynamics of Six Species of Periphyton-Grazing Stream Insects

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A condensation of "Seasonal production dynamics in a guild of periphyton-grazing insects in a southern Appalachian stream." published recently in *Ecology* (Vol. 64, No. 5). The authors are with the Department of Entomology, University of Georgia, Athens. GA 30602.

It has been hypothesized that as a result of competition for food, the periods of maximum resource use by species of stream invertebrates within a functional group will follow a seasonal sequence. and resource overlap among species within functional groups will be minimized. Temporal partitioning has been found to be a predominant mode of ecological segregation among groups of systematically related stream insects. We extended this concept to a functionally similar but systematically diverse group of species.

We studied the life histories and production ecology of six insect species that graze epilithic algae and associated organic matter in a fourth-order unshaded stream reach in the southern Appalachian Mountains. Four species were caddisflies: *Agapetus* sp., *Glossosoma nigrior* Banks, *Goera fuscula* Banks, and *Neophylax consimilis* Bett. The remaining grazers studied were dipterans: *Blepharicera williamsae* Alexander and a combination of two unidentifiable species, designated *Blepharicera* spp.

The stream, Lower Shope Fork, is located within the US Forest Service's Coweeta Hydrologic Laboratory (Macon County, NC) in the Blue Ridge province of the southern Appalachian Mountains. The stream at the study site flows for 200 m through an open meadow, along which riparian vegetation is cut periodically by the Forest Service. Riffles predominate, with no distinct pools. The substrate is rocky, with boulders (>0.25 m diameter) common, and median substrate size (measured on an areal basis) is 105 mm.

Fifteen randomly placed benthic quadrat samples, each 0.1 m² , were collected biweekly from August 1979 to August
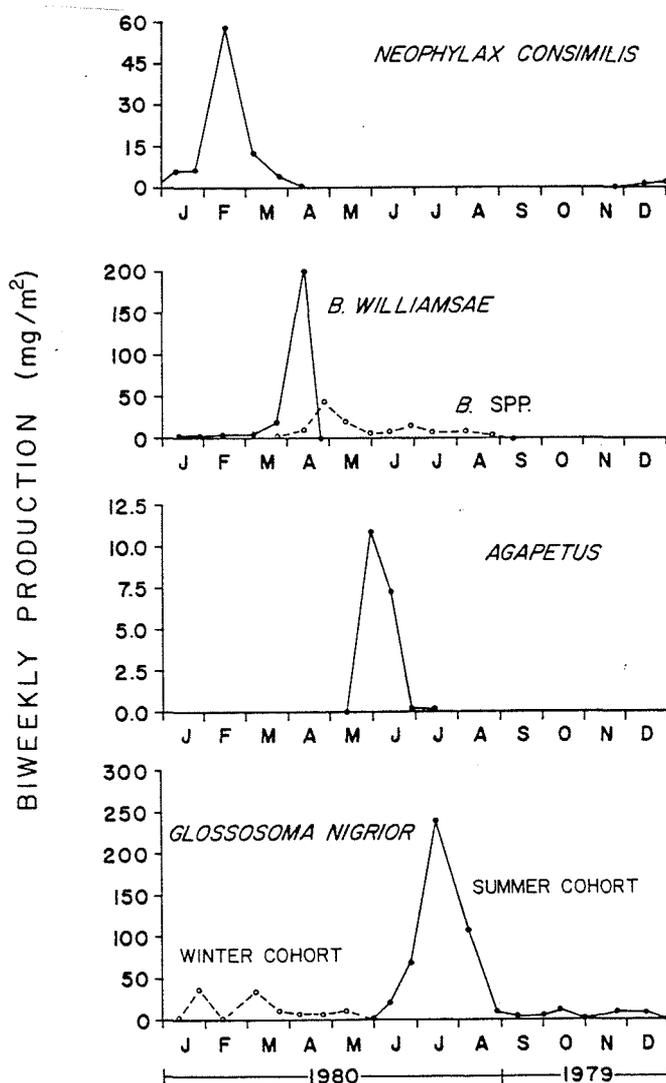

Figure 1. Secondary production by sample interval for five grazer species. Production over each interval was calculated with the instantaneous growth method. Production estimates for *Goera fuscula* were too irregular to plot. Note the differing vertical scales.

to approximately 3 months (winter *Glossosoma* cohort). The longer period of production for *Blepharicera* sp. is expected, since it is a composite of at least two species. The species' production peaks occurred at separate times in the year, with little overlap between species. The winter species, *Glossosoma* (winter cohort), *Neophylax*, and *B. williamsae*, hatched at about the same time in late fall but exhibited different growth patterns. *Glossosoma* grew steadily from January through March, whereas *Neophylax* and *B. williamsae* had maximum production near the end of their larval period (Figure 1). *Neophylax's* specific growth rate was about twice that of *B. williamsae*, so that *Neophylax* production peaked in February to March, whereas most of *B. williamsae*'s production was in late March and April. Production by the spring-summer species was also temporally separated, with *Blepharicera* sp.'s production concentrated in April to May, *Agapetus* in May to June, and the summer *Glossosoma* cohort in July and August.

Comparison with a neutral model indicated that the production peaks of the six species were significantly more regularly spaced ($P < 0.1$) than would be expected by chance alone. Temporal overlap between species was calculated using density, biomass, and production. Overlaps based on density and biomass were similar (means of 0.173 and 0.171 respectively), but mean overlap based on production was significantly lower (0.124).

The patterns of temporal organization observed among these species were linked with specialized life histories. Five species were univoltine, with larval development periods (cohort production intervals, CPI) ranging from 44 to 215 days. The shortest CPIs were associated with species that diapaused in the egg (*Agapetus* sp., CPI = 44 days) or larval stage (*Neophylax consimilis*, CPI = 135 days). *Goera* was too uncommon to permit a quantitative assessment of its life history. Our data indicate that *Goera* fifth instars maintained approximately constant individual mass from November through February, with rapid individual growth from 2–3 to 7–8 mg AFDM in late February and March, which is compatible with other observations of a midwinter larval growth cessation in *G. calcarata*.

Glossosoma did not exhibit a diapause period, but the winter cohort's abundances and production were considerably lower than those of the summer cohort (Figure 1). This asymmetry between the cohorts may be important in *Glossosoma*'s dominance of the scrapers' production, by enabling the species to shift resource use away from the winter months when temporal overlap with other species would be greater.

Absence of canopy cover at the study site presumably results in much higher late spring and summer periphyton growth than would occur in more typically shaded fourth-order streams in the southern Appalachians. Apparently the univoltine species lack the life history flexibility required to take advantage of a locally available resource at an unusual time of year. *Glossosoma* can, in contrast, use the summer periphyton crop without a major alteration of its life history, since its summer cohort is adapted to summer temperature regimes. *Glossosoma*'s bivoltinism, in combination with long periods of diapause in the other species, resulted in a sequence of production by various species throughout the seasons in which the food resource is likely to be most abundant.

Our results support the hypothesis that the species of functional groups within particular stream communities are organized seasonally so as to minimize the periods in which similar resources are being used by two or more species. The possession of life cycles less than a year in duration may be an advantage to organisms in environments with predictable seasonal fluctuations in resource type and availability.

Phosphorus Dynamics in a Woodland Stream Ecosystem

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The term *spiraling* has been used to describe the combined processes of nutrient cycling and downstream transport in a stream ecosystem. In all ecosystems, nutrients tend to migrate downhill as they cycle. In a spatial sense, the "cycle" does not close, but stretches into a helix, or spiral, winding its way downslope. For most ecosystems, the effect of this downhill movement is adequately represented either as export across an ecosystem boundary or as exchanges between spatially defined compartments. For streams, however, in which nutrient transport is clearly a major integral feature of the ecosystem, it is helpful to address the question of spiraling explicitly, with an approach that unifies the processes of transport and cycling while giving individual recognition to each.

We adapted the spiraling concept as a tool for describing and analyzing phosphorus dynamics in a 120-m reach of Walker Branch, a small woodland stream in Tennessee, during a period of summer base flow. To trace the dynamics of phosphorus, we released 10 mCi of $^{32}PO_4$ to Walker Branch for a period of 30 min, measured the uptake of ^{32}P from the water, and then followed the concentrations of ^{32}P in coarse (>1 mm) particulate organic matter (CPOM), fine (<1 mm) particulate organic matter (FPOM), aufwuchs, grazers, shredders, collectors, net-spinning filter feeders, and predators over a six-week period. Rates of transfer among compartments and rates of downstream transport were estimated by fitting a partial differential equation model of the ecosystem to the data. With the resulting coefficients, the model was run to steady state to estimate standing stocks and fluxes of exchangeable phosphorus. Figure 1 shows the relationship among compartments used in structuring the model.

The resulting description of spiraling is summarized in Table 1. One "cycle" or loop of the spiral is viewed as beginning with the water compartment and ending upon return to the water compartment. On a given loop, a P atom has a probability, b_i, of passing through compartment i ($b_i = 1$ for water), and resides in compartment i for an average time, T_i, before passing to another compartment. While residing in a