Substratum-production relationships in net-spinning caddisflies (Trichoptera) in disturbed and undisturbed hardwood catchments

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Abstract. The effect of substratum on production of two species of net-spinning Trichoptera (Hydropsychidae), Parapsyche cardis Ross and Diplectrona modesta Banks, was examined in two second-order southern Appalachian streams: Hugh White Creek (HWC), a reference stream draining an undisturbed hardwood catchment, and Big Hurricane Branch (BHB), which drains a catchment that was clear cut during the first six months of the study. Surber samples were collected monthly for 21 months in four common substrata in each stream: moss-covered rock face, cobble riffle, pebble riffle, and sandy reach.

Both hydropsychid species showed distinct substratum preferences. Abundances and production (size-frequency method) of P. cardis were significantly higher in rock face > cobble riffle > pebble riffle > sandy reach in both streams. Distribution of D. modesta was more uniform among substrata and differed between streams: highest abundances and production occurred in cobble riffle in HWC, but on rock face in BHB; the lower density of moss in HWC may not have provided sufficient microhabitats for Diplectrona compared with the thicker moss of BHB.

Overall production (weighted according to the relative proportions of each substratum in each stream) of D. modesta was highest in HWC. Parapsyche cardis had higher substratum-specific production in BHB than in HWC for all substrata, but higher overall production in HWC; this difference was due to availability of preferred substrata in the two streams. Differences in production between streams may be related more to geomorphic differences (i.e., relative proportion of common substrata) between streams than to effects of logging on these two species. Comparisons between streams on a reach or catchment basis should consider carefully whether the streams differ in geomorphic characteristics such as the relative proportion of channel substrata.

Key words: stream, freshwater invertebrates, secondary production, substratum, filter feeders, Hydropsychidae, Trichoptera, disturbance, clear cutting.

Streambed substratum affects the distribution and abundance of lotic invertebrates (reviewed by Minshall 1984) and can mediate invertebrate response to disturbance (Gurtz and Wallace 1984). Factors that affect substratum-specific estimates of abundance or production include particle size, current velocity, and physical stability, as well as food availability. Estimates of secondary production of aquatic insects can vary significantly among different substrata (Benke et al. 1984, Hall et al. 1980, Resh 1977, Smock et al. 1985, Wallace and Gurtz 1986). Comparisons of production between two streams may need to take substratum into account: for example, changes in production of baetid mayflies in response to catchment logging, compared to a nearby reference stream, differed considerably among four substrata (Wallace and Gurtz 1986). Hence, geomorphic characteristics such as the proportion of various substrata can affect overall estimates of production in a stream reach.

Net-spinning Trichoptera (Hydropsychidae) have strong species- (and often instar-) specific substratum preferences, e.g., particle size, current velocity, density of moss, and microlocation on the substratum (Haefner and Wallace 1981, Malas and Wallace 1977). Filter-feeding caddisflies are sensitive to alterations in food quantity and quality that may occur throughout upstream reaches (not just localized effects) as a result of a major catchment disturbance. Thus, hydropsychids are appropriate species for examining relative differences between streams, in production or densities, on a substratum-specific basis. Our study examines secondary production of two species of Hydropsychidae—Parapsyche cardis Ross and Diplectrona mo-
desta Banks—in four substrata in two southern Appalachian streams, one of which drains a catchment that was clear cut at the beginning of the study.

Methods

Study site

The research was conducted at Coweeta Hydrologic Laboratory in the southern Appalachian Mountains near Otto, North Carolina. Hugh White Creek (HWC) drains a reference watershed (WS 14) that has mixed hardwood vegetation. Big Hurricane Branch (BHB) drains WS 7, which is separated from WS 14 by ca. 1.4 km. Clear cutting of WS 7 took place between January and June 1977, primarily by a mobile cable system. Before the clear cut, vegetation in the two watersheds was similar, dominated by an oak-hickory association at intermediate elevations; tulip poplar, eastern hemlock, and red maple occurred at lower elevations and lower ravines. Streamside vegetation, dominated by Rhododendron maximum, provided dense shading of both streams initially, but the riparian canopy of BHB following logging was much less dense than that of HWC.

Sampling

Replicate Surber samples (0.09 m²; mesh opening 300 µm) were collected monthly (three in HWC, four in BHB) in each of four common substrata during January 1977 to September 1978 (n=12/month in HWC, n=16/month in BHB). A randomized complete block design was used. Blocks were of four common substrata defined by predominant particle size: rock face (granitic outcrops, exposed bedrock, or large boulders, usually with a moss cover), cobble riffle, pebble riffle, and sand (Gurtz and Wallace 1984). Samples were preserved in the field with 4% formaldehyde solution; invertebrates were picked in the laboratory at 7x magnification. For detailed descriptions of study streams, the experimental logging procedure, and sampling methods, see Gurtz and Wallace (1984) and Webster et al. (1983).

Production estimates

Production was estimated by the size-frequency method of Waters and Hokenstrom (1980). Size classes were larval instars, determined according to head capsule widths measured across the eyes with an ocular micrometer. Confidence intervals were estimated according to the method of Krueger and Martin (1980). Biomass (ash-free dry mass; AFDM) was obtained from instar-biomass relationships developed from other studies in Coweeta streams (D. H. Ross and A. D. Huryn, University of Georgia, unpublished data); data were combined for several streams over four seasons to minimize potential errors in mean weight estimates.

Results

Life cycles

Life cycles of both Parapsyche and Diplectrona were similar to those reported by Benke and Wallace (1980) in a fourth-order southern Appalachian stream and by Haefner and Wallace
Diplectrona modesta

in Hugh White Creek and Big Hurricane Branch for each of four substrata. Standard errors are shown in parentheses.

<table>
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<th>Instar III</th>
<th>Instar IV</th>
<th>Instar V</th>
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Distribution of Diplecotrona among substrata, however, differed between the two streams and among instars. In HWC, Diplecotrona was significantly most abundant in cobble riffle samples and least abundant in rock face samples; first instars appeared to prefer sand, while all other

The order of abundances among substrata was the same for each instar in each stream. Distribution of Diplecotrona among substrata, however, differed between the two streams and among instars. In HWC, Diplecotrona was significantly most abundant in cobble riffle samples and least abundant in rock face samples; first instars appeared to prefer sand, while all other
instars preferred cobble riffle. In BHB, Diplectrona distributions did not differ significantly among substrata, although sand had lowest abundances (Duncan’s multiple range test on log-transformed data, $p > 0.05$). Instars I, II, and III were much more abundant on rock face than other substrata, but instars IV and V were more evenly distributed among substrata.

**Production**

Estimates of production in each substratum as well as overall production (calculated from abundances weighted according to the amount of each substratum in each stream) followed trends among substrata and between streams similar to estimates of density (Fig. 1). The relative importance of substratum for Parapsyche was the same in each stream: rock face > cobble riffle > pebble riffle > sandy reach. Production in the rock face substratum was ca. 200× higher than in sandy reach and accounted for 94.8% of total Parapsyche production in HWC and 87.3% in BHB, based on proportional areas of substratum. Parapsyche production (weighted estimate) was higher in HWC than in BHB, even though production in individual substrata was lower in HWC in all cases. The greater proportion of rock face and boulder substrate in HWC (36.5% of stream channel) compared to BHB (16.8%) more than compensated for the lower substratum-specific production in HWC.

Production of Diplectrona was more uniformly distributed among substrata, and the most productive substratum differed for the two streams: cobble riffle in the reference stream (HWC) and rock face in the clear-cut stream (BHB). In contrast to Parapsyche, rock face accounted for only 7.0% of total Diplectrona production in HWC and 29.7% in BHB. Cobble riffle contributed 53.9% of the production of Diplectrona in HWC, but only 18.7% in BHB. Overall, production of Diplectrona was higher in BHB than in HWC.

We have used 21-month (593 d) values for most comparisons in order to use fully all available data during and following logging of the BHB catchment. Multiplying data shown in Figure 1 by the ratio 365/593 yields an annual estimate of production. These annual values include the period October to December only once, whereas other months are included twice; because all instars of Diplectrona and instars II-V of Parapsyche were present during those months, these values may be reasonably valid estimates of annual production. Annual production estimates reported here did not differ greatly from values based on a 24-month period, with October to December 1977 represented twice.

Total (weighted) production for these two species in BHB was 2.7 g AFDM/m² for the 21-month period (equivalent to 1.7 g “annual” production), of which 77.0% was due to Parapsyche. In HWC, total production was 2.8 g AFDM/m² for the 21-month period (1.8 g “an-
nal” production), 94.8% due to Parapsyche. Parapsyche production exceeded that of Diplectrona for all substrata in both streams.

Discussion

Our findings support the contentions of other recent studies (e.g., Benke et al. 1984, O’Hop et al. 1984, Smock et al. 1985; Wallace and Gurtz 1986) that substratum is a key parameter to be considered in production studies. In our study, despite a major disturbance (clear cutting) on one of the catchments, there was greater similarity between streams than among substrates.

Weighted annual production of Diplectrona in HWC (0.090 g AFDM/m²) is within the range of annual values in other studies of undisturbed streams (0.097 [dry weight], Cushman et al. 1977; 0.270, Haefner and Wallace 1981; 0.031–0.244, Ross and Wallace 1983), but production of Parapsyche in HWC (1.66) was somewhat higher than in other Coweeta streams that did not have as much rock outcrop substratum at the sampling sites (1.19, Haefner and Wallace 1981; 0.16–0.98, Ross and Wallace 1983). Overall production in BHB for both Diplectrona (0.39) and Parapsyche (1.29) was less than corresponding values in a nearby catchment that had been previously clear cut (Diplectrona: 0.65, Parapsyche: 4.27; Haefner and Wallace 1981).

The most important substratum in production of these species was moss-covered outcrop (rock face), except for Diplectrona in HWC. The lower density of moss in HWC may not have provided sufficient microhabitats for Diplectrona compared with the thicker moss of BHB; Diplectrona prefers slower current velocities than Parapsyche (Malas and Wallace 1977, Wallace et al. 1977), and abundances of Diplectrona were positively correlated (p < 0.001) with the amount of moss in BHB, but not in HWC. Moss also provides substratum for attachment of retreats and nets.

Substratum-weighted mean production of Parapsyche was not significantly different between HWC and BHB (p > 0.05), but Diplectrona production was significantly higher in BHB than in HWC. This corresponds generally with conclusions based on tests for trends in abundance in BHB compared to HWC for the 21-month study period (Gurtz and Wallace 1984), which showed no significant (p > 0.10) trends for Parapsyche in any substratum, but an increasing trend (p < 0.10) for Diplectrona in cobble riffle; a significant decreasing trend was also found for Diplectrona in sand, but this substratum contributed less than cobble to total production of this species.

Abundance and production data provided similar patterns among substrata and between streams, unlike some other studies (e.g., O’Hop et al. 1984). This relationship should be expected for univoltine species when weights or CPI differ little among treatments. Other factors which may have contributed to production included somewhat faster growth rates in the clear-cut stream as reflected in the shorter CPI, which was primarily responsible for the higher R/B ratios in BHB (Parapsyche: 5.4, Diplectrona: 5.5) compared to HWC (Parapsyche: 4.6, Diplectrona: 4.3). Growth rates may have been influenced by warmer water temperatures or potentially higher food quality in the clear-cut stream. These differences affected substratum-specific production, but were outweighed by geomorphic differences in terms of overall production.

Differences in production between streams may be related more to differences in relative proportion of substrata than to effects of logging on these two species. This contrasts with responses of some other taxa for which substratum-specific trends in abundance (Gurtz and Wallace 1986) or production (of baetid mayflies; Wallace and Gurtz 1986) in BHB compared to HWC were attributed to logging.

In another Coweeta study, production of both Parapsyche and Diplectrona were much higher in a stream draining a clear-cut catchment after 10 years of succession than in a nearby reference stream (Haefner and Wallace 1981). Our findings in the present study are in general agreement for Diplectrona, but overall (weighted) production of Parapsyche in our clear-cut stream (BHB) was less than in the reference stream (HWC). The reason for this difference may be in the relative proportions in each stream of the rock face substratum, where high substratum-specific production may have been enhanced in the clear-cut streams by increased organic seston (Gurtz et al. 1980; Webster and Golladay 1984) and higher delivery rate (particles and drifting animals per time for a given area of net opening) over outcrops (Smith-Cuffney and Wallace 1986), as well as high densities in BHB of potential prey taxa (especially collector-gatherers) for filter feeders (Gurtz and
In the Haefner and Wallace (1981) study, the clear-cut stream contained proportionately over twice as much moss-covered outcrop substrate as the reference stream, whereas in our study the reverse was true. Thus, the opposite patterns found in these two studies for production of *Parapsyche* in the clear-cut stream compared to the reference may be attributed to geomorphic differences in the streams rather than differences due to the clear cut.

Stratified random sampling designs based on substrata can have several advantages over sampling of a single substratum or strictly random sampling. Comparisons of production estimates between streams based on only one substratum may yield incorrect or misleading results unless there are preliminary data on relative production and availability of substrata in each stream. These considerations are especially important if interpretation is to be extended from the sampling unit to a stream reach or catchment. Random sampling may yield similar overall estimates on a reach or catchment basis; however, with a substratum-stratified design, fewer samples may be required to achieve the same or greater accuracy if the population is aggregated (Lamberti and Resh 1979). In our study, 87% of the production of *Parapsyche* in BHB occurred on rock face and boulder substrata, which accounted for only 17% of the overall substratum; corresponding values for HWC are 95% of the production and 37% of the substratum. When one substratum contributes a disproportionate share of the total stream production for a species, a random sampling regime might underestimate total production unless a large number of samples were taken.

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**Literature Cited**


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