4 High-Gradient Streams of the Appalachians

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The southern Appalachian region encompasses portions of nine states: West Virginia, Maryland, Virginia, Kentucky, Tennessee, North and South Carolina, Georgia, and Alabama. Within this region of abundant rainfall, extensive forests, and rugged terrain, many streams originate, serving a growing and diverse assemblage of interests, such as municipal, manufacturing, hydroelectric, and recreational needs. This region includes the headwaters, or portions of headwaters, of many rivers, including the Potomac, Ohio, James, Roanoke, Yadkin-Pee Dee, Santee, Savannah, Chattahoochee–Apalachicola, Alabama, and Tennessee. Water originating from these watersheds constitutes an important resource for major metropolitan areas. Thus, management of headwater streams and their watersheds is vital to the rapidly growing population of the region.

The major objectives of this chapter are to (1) synthesize our current knowledge relative to the biotic structure and function of high-gradient streams in the Southeast; (2) identify factors that control or regulate biotic structure and function in these systems; (3) evaluate the impact of various management (and mismanagement) practices on the biota of streams within the region; and, (4) address immediate and long-term research needs for high-gradient streams. We characterize high-gradient streams as those with longitudinal gradients exceeding 0.15% slope within the Blue Ridge and Ridge and Valley provinces. Many streams draining the Piedmont Plateau have reaches with slopes far exceeding 0.15% especially in the vicinity of the fall line, and these systems are addressed elsewhere in this book (see Mulholland and Lenat, 133).
Chapter 5). Although slopes of 0.15% may appear low for high-gradient streams, larger fifth- and sixth-order streams of tortuous whitewater rivers, such as the Chattooga (Georgia—South Carolina) and the Ocoee (Tennessee), have gradients of only 0.5–1.1%. In contrast, many small headwater (first- and second-order) streams of the southern Appalachians have gradients exceeding 30%.

PHYSIOGRAPHY OF THE REGION

In the Appalachian region, climate, lithology, and relief display considerable variation. Each of these components of the physical environment influences the structure of biotic communities of streams within this region. The southern Appalachian region consists of a series of different geological provinces, including the Blue Ridge, Ridge and Valley, and the Cumberland and Allegheny plateaus (Fig. 1). The Blue Ridge province extends from northern Georgia to southern Pennsylvania and is bordered on the east by the Piedmont Plateau. In most locations the Blue Ridge Escarpment rises abruptly from the lower Piedmont Plateau (Fig. 2). A dense deciduous forest covers much of the Blue Ridge, and in the southern section a coniferous forest consisting of Fraser fir, *Abies fraseri*, and red spruce, *Picea rubens*, constitutes the dominant vegetation near the crests of the higher mountains. Slopes are generally steep, with many exceeding 30% (Fenneman 1938).

The Ridge and Valley province, extending from the Coastal Plain in Alabama to the St. Lawrence Valley in the north, borders the western side of the Blue Ridge province (Fig. 1, Fenneman 1938). The Ridge and Valley province is characterized by long, narrow, rather even-topped ridges with streams in valley floors. Streams have played a major role in shaping the present topography (Fenneman 1938, Hack 1980). Streams in the Ridge and Valley Province follow primarily belts of nonresistant rock and display a distinct trellised pattern.

The Appalachian plateaus (Cumberland in the south and Allegheny in the north) border the western side of the Ridge and Valley province. Overall, the elevations of the Appalachian plateaus decline from the east toward their western side. Some spectacular river gorges, such as that of the New River are found in the Allegheny region. Farther south in extreme southwestern Virginia, eastern Kentucky and Tennessee, and northern Alabama, the Cumberland Mountains and Cumberland Plateau constitute the southern portion of the Appalachian plateaus. The Cumberland mountains represent a narrow region in eastern Kentucky, eastern Tennessee, and southwestern Virginia and they constitute the main divide between the Ohio and Tennessee rivers. The Cumberland Mountain section is analogous to the Allegheny Front farther north (Fenneman 1938). Although rock types in the Cumberland Plateau tend to be more resistant than in the Allegheny Plateau, the boundary between the two areas is somewhat arbitrary (Fenneman 1938).
Climate

Summer temperatures in the region are generally cool and the winters are relatively mild (Table 1). Temperatures at a given latitude are strongly influenced by elevation, as temperature decreases about 1.8 °C for each 305-m increase in altitude. Thus, some of the higher peaks in the southern Appalachians, such as Mount Mitchell (>1800 m), Grandfather Mountain in North Carolina, and Clingman’s Dome (>1800 m) in Tennessee may have cooler temperatures than regions found much farther north. Groundwater and springs tend to maintain a rather constant year round temperature close to the mean annual temperature of the region. Depending on elevation, small streams and spring runs where flows are strongly influenced by groundwater display a winter temperature (Vannote and others compare to bama. Down ample, at the headwaters i annual temp annual degree days has an annual degree days. Rainfall is to over 200 cm/year at the southwestern where the b (Table 1). Southeastern and in most

Hydrology

Because of streams, par extended dr year and sea of the terres Lowest flow associated w

For stream flow/ Most of this Quick flow Appalachia

Logging (e.g., Hewlett flow results e.g., Hibber influence st reduces ann and Dougla
PALACHIANS

high-gradient water rivers, (Tennessee), water (first-gradients ex-

considerable nt influences on the lower ng of Fraser he dominant terally steep,

Plain in Al- stern side of id Allegheny ern Georgia nont Plateau. on the lower h of the Blue ng of the Blue Ridge and he dominant sharply steep,

Plains in Allegheny the northwestern la, the Cum- ng of the Blue Ridge and the dominant sharply steep,

FIGURE 2. Profiles of the New and Yadkin Rivers from their common divide along the Blue Ridge escarpment in western North Carolina. (Redrawn from Hack 1969.)

TABLE 1 Temperature and Precipitation from Various Locations in the Southern Appalachians

<table>
<thead>
<tr>
<th>Location (State/Local)</th>
<th>Elevation (m)</th>
<th>Mean Annual Temperature (°C)</th>
<th>Mean Monthly Temperature (°C)</th>
<th>Precipitation Mean Annual (cm)</th>
<th>Percentage of Annual as Frozen*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maryland Oakland</td>
<td>737.6</td>
<td>8.7</td>
<td>-2.8</td>
<td>19.7</td>
<td>119.7</td>
</tr>
<tr>
<td>West Virginia</td>
<td>White Sulfur Springs</td>
<td>585.2</td>
<td>11.6</td>
<td>0.2</td>
<td>22.4</td>
</tr>
<tr>
<td>Virginia</td>
<td>Big Meadows</td>
<td>1077.5</td>
<td>8.6</td>
<td>-2.1</td>
<td>19.2</td>
</tr>
<tr>
<td></td>
<td>Floyd</td>
<td>792.5</td>
<td>11.2</td>
<td>0.9</td>
<td>21.3</td>
</tr>
<tr>
<td></td>
<td>Pennington Gap</td>
<td>460.2</td>
<td>12.4</td>
<td>1.3</td>
<td>22.8</td>
</tr>
<tr>
<td>North Carolina</td>
<td>Grandfather Mountain</td>
<td>&gt;1610</td>
<td>5.7</td>
<td>-2.9</td>
<td>16.7</td>
</tr>
<tr>
<td></td>
<td>Coweeta Hydrologic Lab.</td>
<td>679.0</td>
<td>13.0</td>
<td>3.2</td>
<td>21.6</td>
</tr>
<tr>
<td></td>
<td>Coweeta Hydrologic Lab.</td>
<td>1364</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Tennessee</td>
<td>Crossville</td>
<td>551.7</td>
<td>12.1</td>
<td>0.5</td>
<td>22.6</td>
</tr>
<tr>
<td></td>
<td>Blairsville</td>
<td>584.3</td>
<td>12.6</td>
<td>2.6</td>
<td>22.4</td>
</tr>
<tr>
<td>Alabama</td>
<td>Valley Head</td>
<td>317.0</td>
<td>14.3</td>
<td>3.3</td>
<td>24.6</td>
</tr>
</tbody>
</table>

*Based on a conversion of 10 to 1 (snow to rainfall).
•Based on 45–50 years of record; complete temperature records for the high-elevation station are not available.

Source. From NOAA (1980) and records of the Coweeta Hydrologic Laboratory.
display a wide range of temperature regimes within an area. Groundwater temperatures closely approximate mean annual temperature of the region (Vannote and Sweeney 1980). Thus, a headwater stream near the summit of some of the high-elevation mountains in North Carolina and Tennessee may accumulate only about 2200 degree days per year (mean temperature \( \times 365 \)) compared to some 5000+ degree days for similar streams in northern Alabama. Downstream, annual temperature variation tends to increase. For example, at the Coweeta Hydrologic Laboratory in the Little Tennessee River headwaters in western North Carolina, high-elevation (>1200 m) springs have annual temperature ranges of about 6.7 to 12.8 °C and accumulate about 3450 annual degree days. Downstream at an elevation of 865 m, a fourth-order reach has an annual range of 0 to 21 °C and accumulates about 4150 annual degree days. Farther downstream the little Tennessee River (elev. = 537 m) has an annual temperature range of 0 to 27 °C and accumulates around 5000 annual degree days (J. B. Wallace and North Carolina Department of Natural Resources, unpublished data).

Rainfall is abundant throughout the region, ranging from about 100 cm/year to over 200 cm/year. The highest rainfall in eastern North America occurs in southwestern North Carolina, western South Carolina, and northeastern Georgia where the boundaries of the three states meet; for example, note the 238 cm/year at the higher elevation site within the Coweeta Hydrologic Laboratory (Table 1). Seasonally, rainfall is fairly evenly distributed throughout the region and in most locations less than 10% of the total precipitation is frozen.

**Hydrology**

Because of abundant rainfall, most streams are permanent, though some streams, particularly those in limestone areas, may occasionally dry up during extended droughts. Precipitation is fairly evenly distributed throughout the year and seasonal differences in baseflow discharge reflect evapotranspiration of the terrestrial vegetation, with highest baseflow in winter and early spring. Lowest flows typically occur in later summer and early autumn. High discharge associated with storms may occur at anytime of the year.

For streams with forested mountain watersheds, annual water yield (annual stream flow/annual precipitation over the watershed) averages about 40–60%. Most of this occurs as base or delayed flow (Woodruff and Hewlett 1970). Quick flow averages around 4–12% of annual stream flow in the southern Appalachians (Woodruff and Hewlett, 1970).

Logging or other removal of vegetation results in increased stream flow (e.g., Hewlett and Hibbert 1961, Swank et al. 1988). The increased stream flow resulting from forest cutting declines with time as the forest regrows (e.g., Hibbert 1966, Swift and Swank 1981). The type of forest cover can also influence stream flow. For example, converting deciduous hardwoods to pine reduces annual stream flow by 20% in the southern Appalachians (Swank and Douglass 1974).
Geology

The prolonged and diverse mountain formation period in the southern Appalachians has produced bedrock patterns that are complex, both locally and regionally (Hack 1969, King 1977, and Chapter 2, this volume). Most of the interior of the Appalachians in the southeast had been thoroughly deformed and consolidated by mid-Paleozoic time. The sedimentary Appalachians, to the west of the crystalline Appalachians, were formed during the later Paleozoic phase. The Paleozoic period of Appalachian formation has been followed by perhaps 200 million years of downwasting or erosion (Hack 1969, King 1977). Different rock types forming the Appalachians have resulted in asymmetrical stream and mountain slopes in many areas. The Blue Ridge Escarpment (eastern continental divide, Atlantic and Mississippi drainage system) is clearly asymmetric in North Carolina (Hack 1969, and Fig. 2). The Yadkin River originates on the southeastern side of the escarpment where it has a very steep gradient that decreases greatly once it reaches the Piedmont where the river flows across nonresistant rocks (primarily gneisses and schists). In contrast, the New River flows northwest, crossing extensive areas of rock containing quartz veins, which are more resistant to chemical and mechanical weathering (Hack 1969). Farther downstream, in the vicinity of the Great Valley, the New River crosses large areas of quartzites and sandstones and maintains a steep gradient for a river of large discharge and length. The divide appears to be migrating westward as a result of erosion and uplift (Hack 1969, 1980). This migration is believed to have resulted in a series of stream captures and major modifications of drainage systems (Fenneman, 1938, Ross 1969).

Even large topographic features of the Appalachian Highlands are attributable to differential erosion of rocks of different resistance, and the major drainage systems of the region have become closely adjusted to rock type (Hack 1980). Most areas of high relief and high altitude have been formed on resistant rocks. In contrast, the Cambrian and Ordovician belt, extending from Alabama to the Canadian border on the western side of the Blue Ridge, contains mostly shale and carbonate rocks, which are less resistant to weathering.

Channel slopes in the smaller headwater streams are normally inversely related to discharge, and because discharge and length are directly related, channel slopes are generally inversely proportional to stream lengths. Thus, most longitudinal stream valley profiles assume a concave form (Hack 1980). However, the overall channel slope is strongly influenced by underlying rock type (Hack 1973). According to the hypothesis presented by Hack (1980), profiles of the major Appalachian rivers are explained in part by adjustments as streams cross downstream areas of resistant rock. The resistant downstream bedrock forms local base levels at different altitudes that influence upstream profiles. Major river systems penetrating the Appalachian Highlands show large differences in profile and altitude along reaches of Cambrian and Ordovician rocks, while all have headwater reaches in more resistant rock (Hack...
1980). Rock types have important influences on local relief and landscape forms and water chemistry. Hack (1969) summarized some of the characteristics of the predominant rock types of the southern Appalachians as follows:

1. **Granites and other light-colored, course-grained, crystalline rocks.** Are fairly resistant to erosion and water penetration and tend to form areas of steep slopes. These rocks erode primarily by mechanical chipping.

2. **Mica schists.** Tend to occupy areas of low relief in the Blue Ridge, since they are generally very susceptible to chemical and mechanical weathering.

3. **Sandstone and quartzites.** Are resistant to both chemical and mechanical weathering. These rocks tend to form ridges in the Appalachian Valley, are the underlying rock of plateau tops in the Cumberlands, and are usually found in areas of steep slopes. Streams flowing through sandstones and quartzites are lined with cobbles and boulder substrate.

4. **Carbonate rocks.** Include limestone and dolomite, which react with weak acids in rainwater, soil, or groundwater. The limestone, or dolomite, is dissolved and components are transported in solution. Some limestones contain silica and calcium sulfates, which results in higher relief than belts of pure limestone.

5. **Shale.** A nonresistant rock, which is easily penetrated by water, decomposes readily into smaller fragments, and tends to form areas of relatively low relief and thin soils.

Geologic structure influences water chemistry, drainage basin patterns, hydrologic behavior, local substrate, slope, and longitudinal profiles of the streambed. These, in turn, influence the distribution, abundance, and productivity of the stream flora and fauna. Hence, the local geomorphic processes that occurred some 200–300 million years ago exert strong influence on present stream biota and processes.

High-gradient mountain streams of the Blue Ridge, or crystalline Appalachians, are typically dendritic. Stream density may be as high as 6.2 km/km² (Harshbarger 1978). In the ridge and valley, or sedimentary Appalachians, streams may have a dendritic pattern, but downstream they tend to follow a somewhat trellised pattern. Gradients may be greater than 20% in some small streams, but vary considerably depending on geological characteristics. In the Ridge and Valley province, adjacent valleys, one principally limestone and the other shale, may have very different stream gradients.

**Chemical Environment**

Baseflow concentrations of most ions, for example, Cl⁻, K⁺, Na⁺, Ca²⁺, Mg²⁺, and SO₄²⁻ are usually low (<1 mg/L) and concentrations of nutrients.
such as NO$_3$-N, NH$_4$-N, and PO$_4$-P may be very low (0.001–0.004 mg/L for each) in undisturbed streams draining the crystalline Appalachians (Swank and Douglass 1977, Silsbee and Larson 1982). Bedrock geology, elevation, and disturbance history influences nutrient concentrations. The pH of most streams in the crystalline Appalachians is circumneutral (ca. 7.0) and Messer et al. (1986) found that less than 3.2% of stream sites in the Blue Ridge had pH values below 6.4. However, Silsbee and Larson (1982) reported lower pH values (e.g., 5.2–5.5) in streams draining watersheds with the Anakeesta formations (Silsbee and Larson 1982). Anakeesta groups contain pyrites and other sulfides which form dilute sulfuric acid solutions, resulting in lowered pH and alkalinity, and increased conductivity and magnesium concentrations. Similar pyritic rocks occur in other areas of the Appalachians (see Silsbee and Larson 1982). During episodic rain storms or snow melt pH can be depressed rapidly. In Raven Fork, North Carolina, pH occasionally decreased to below 5.0 during storms and, during the same periods, total monomeric aluminum concentrations increased from <50 to >350 µg/L (Jones et al. 1983). Stream pH, alkalinity, Si, K, Na, and turbidity decrease with increasing elevation in the Great Smoky Mountain National Park, whereas nitrate concentrations increased with elevation (Silsbee and Larson 1982). In undisturbed streams in the Coweeta Basin of western North Carolina, highest values for nitrates and sulfates were also found in higher elevation catchments (Swank and Douglass 1977). Clear-cutting and logging also influence nutrient concentrations. Logged catchments in various stages of natural revegetation show elevated nitrate concentrations for at least 10 years following cutting, but appear to return to baseline levels within two decades of regrowth (Swank and Douglass 1977).

Kaufmann et al. (1988) provided an extensive chemical survey of streams draining various geological provinces in the eastern United States. Their results indicate the general tendency for concentrations of many chemicals as well as acid-neutralizing capacity (ANC), conductivity, pH, and total base cations to increase downstream (Table 2). Compared with other Appalachian regions, the southern Blue Ridge has lower ANC, calcium, conductivity, dissolved organic carbon, bicarbonate, nitrate, sulfate and total base cations (Table 2). In contrast to the slow weathering rate of crystalline rock, sedimentary rocks such as limestones have faster weathering rates, which result in streams with higher concentrations of dissolved substances. Alkalinity, pH, and concentrations of nutrients are usually higher in limestone drainages (Table 3).

Many management practices influence water quality of Appalachian streams, such as clear-cutting, surface mining and acid mine drainage, industrial and municipal wastes, riparian disturbances, agricultural practices, impoundments, and the potential problem of acid precipitation, which will be discussed at the end of this chapter. The U.S. Geological Survey Water-Data Reports for the various states are good sources for additional information on stream chemistry in various areas of the Appalachians.
### TABLE 2 Means of Selected Chemical Characteristics of Some Appalachian Streams

<table>
<thead>
<tr>
<th>Chemical Parameter</th>
<th>Units</th>
<th>Upper Reach</th>
<th>Lower Reach</th>
<th>Upper Reach</th>
<th>Lower Reach</th>
<th>Upper Reach</th>
<th>Lower Reach</th>
</tr>
</thead>
<tbody>
<tr>
<td>ANC&lt;sup&gt;a&lt;/sup&gt;</td>
<td>(µeq/L)</td>
<td>644.8</td>
<td>819.9</td>
<td>241.2</td>
<td>257.2</td>
<td>796.0</td>
<td>1001.8</td>
</tr>
<tr>
<td>Calcium</td>
<td>(µeq/L)</td>
<td>673.9</td>
<td>810.9</td>
<td>173.4</td>
<td>191.9</td>
<td>641.2</td>
<td>833.1</td>
</tr>
<tr>
<td>Conductivity</td>
<td>(µS/cm)</td>
<td>117.6</td>
<td>138.6</td>
<td>29.2</td>
<td>34.7</td>
<td>103.3</td>
<td>129.8</td>
</tr>
<tr>
<td>DOC&lt;sup&gt;c&lt;/sup&gt;</td>
<td>(mS/L)</td>
<td>1.9</td>
<td>1.6</td>
<td>0.6</td>
<td>0.8</td>
<td>1.6</td>
<td>1.7</td>
</tr>
<tr>
<td>Bicarbonate</td>
<td>(µeq/L)</td>
<td>610.5</td>
<td>774.9</td>
<td>214.3</td>
<td>219.2</td>
<td>710.8</td>
<td>928.5</td>
</tr>
<tr>
<td>Potassium</td>
<td>(µeq/L)</td>
<td>33.3</td>
<td>31.9</td>
<td>16.6</td>
<td>18.2</td>
<td>31.1</td>
<td>34.2</td>
</tr>
<tr>
<td>Ammonium</td>
<td>(µeq/L)</td>
<td>2.1</td>
<td>1.5</td>
<td>0.9</td>
<td>1.0</td>
<td>2.6</td>
<td>2.4</td>
</tr>
<tr>
<td>Nitrate</td>
<td>(µeq/L)</td>
<td>92.7</td>
<td>90.6</td>
<td>10.0</td>
<td>12.1</td>
<td>31.5</td>
<td>24.1</td>
</tr>
<tr>
<td>pH</td>
<td>(pH units)</td>
<td>6.0</td>
<td>7.2</td>
<td>6.9</td>
<td>7.0</td>
<td>6.4</td>
<td>6.9</td>
</tr>
<tr>
<td>Phosphorus&lt;sup&gt;f&lt;/sup&gt;</td>
<td>(µM)</td>
<td>0.4</td>
<td>0.3</td>
<td>0.7</td>
<td>1.3</td>
<td>0.4</td>
<td>0.3</td>
</tr>
<tr>
<td>Sulfate</td>
<td>(µeq/L)</td>
<td>246.9</td>
<td>278.0</td>
<td>28.5</td>
<td>39.1</td>
<td>155.9</td>
<td>244.0</td>
</tr>
<tr>
<td>Base Cations&lt;sup&gt;g&lt;/sup&gt;</td>
<td>(µeq/L)</td>
<td>1148.1</td>
<td>1384.1</td>
<td>307.0</td>
<td>338.2</td>
<td>1049.3</td>
<td>1341.0</td>
</tr>
</tbody>
</table>

Note. The data include upper and lower reaches of various streams. Only means for the various streams are given here and in many cases standard deviations within a region are high.

<sup>a</sup>Includes northern and western Virginia, western Maryland, and southern Pennsylvania.

<sup>b</sup>Includes Georgia, South Carolina, Tennessee, and southwestern North Carolina.

<sup>c</sup>Includes southern Ridge and Valley (Alabama, Georgia, Tennessee), Cumberland Plateau (Tennessee, Alabama), central Blue Ridge (North Carolina, Virginia).

<sup>d</sup>ANC, acid-neutralizing capacity.

<sup>e</sup>DOC, dissolved organic carbon.

<sup>f</sup>Total dissolved phosphorus.

<sup>g</sup>Total base cations.

Source. Data from Kaufmann et al. (1988).
TABLE 3 Comparison of Nutrient Concentrations of Stream Water from Control Catchments at the Coweeta Hydrologic Laboratory in Western North Carolina with Those of Walker Branch in Eastern Tennessee

<table>
<thead>
<tr>
<th>Item</th>
<th>Coweeta</th>
<th>Walker Branch</th>
</tr>
</thead>
<tbody>
<tr>
<td>pH of streamwater</td>
<td>6.64</td>
<td>7.6</td>
</tr>
<tr>
<td>NO₃-N</td>
<td>5 ppb</td>
<td>13.0 ppb</td>
</tr>
<tr>
<td>NH₄-N</td>
<td>4 ppb</td>
<td>22 ppb</td>
</tr>
<tr>
<td>PO₄-P</td>
<td>1–2 ppb</td>
<td>2 ppb</td>
</tr>
<tr>
<td>K</td>
<td>0.3–0.4 ppm</td>
<td>0.7 ppm</td>
</tr>
<tr>
<td>Na</td>
<td>0.8 ppm</td>
<td>0.6 ppm</td>
</tr>
<tr>
<td>Ca</td>
<td>0.5–0.6 ppm</td>
<td>24.5 ppm</td>
</tr>
<tr>
<td>Mg</td>
<td>0.3 ppm</td>
<td>13.3 ppm</td>
</tr>
</tbody>
</table>

Note. The underlying rock of the Coweeta Basin is pre-Cambrian gneiss and that of Walker Branch is Knox dolomite of Cambrian and Ordovician age.

Data from Swank and Douglas (1977).
Data from Elwood and Nelson (1972) and Elwood and Henderson (1975).

PLANT COMMUNITIES AND ENERGY SOURCES

In general, high-gradient streams of the southeastern United States support a reduced flora relative to lentic habitats and low-gradient streams. A majority of the high-gradient streams occupy watersheds that are not suitable for agriculture and are therefore densely shaded by riparian vegetation (Fig. 3a, b). A second factor that limits the stream flora is the high current velocity, which forces most autotrophs to be intimately substrate associated and eliminates many microhabitats such as planktonic or epipelic. Although this results in reduced standing crops and a limited flora, rheophilous communities often contain the most characteristic and endemic species in a region (Patrick 1948).

Vascular Plants and Bryophytes

To survive in fast-flowing water, vascular plants must have adventitious roots, rhizomes (stolons), flexible stems, and streamlined narrow leaves (Westlake 1975). *Podostemum ceratophyllum* Michx. exemplifies the morphology necessary to occupy high-gradient streams. Attaching to rocks with disk-like processes and giving rise to linearly divided leaves, *Podostemum* is usually found in clear streams with good aeration. Although *Podostemum* is seldom reported since it occurs in swift, usually "white water" (Fassett 1966), Meijer (1975) documented its broad distribution in the southern Appalachian Mountains and suggested that it is an indicator of clean streams in the region. *Podostemum* is the dominant macrophyte in the New River and contributes...
FIGURE 3. Some typical Appalachian streams. (A) Hugh White Creek, a second-order stream at the Coweeta Hydrologic Laboratory in western North Carolina. Note the dense riparian rhododendron. (B) A larger, fifth-order stream in the Great Smoky Mountains National Park. Note absence of dense rhododendron canopy.

FIGURE 4. Great Smoky boidea (at 15) (Photos suppl)
ates support
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ick 1948).

thetic roots,
ology nec-
th disk-like
is usually
is seldom
966), Meijer
hian Moun-
the region.
 contributes
significantly to the river’s organic matter budget (Hill and Webster 1984),
generally entering the food chain as an autumnal pulse of rapidly decomposed
detritus (Hill and Webster 1982b, 1983).

The water willow, *Justicia americana* (L.) Vahl., is also an important ma-
crophyte of southeastern streams. Unlike *Podostemum, Justicia* is rooted in
the sediments (Schmalzer et al. 1985), which excludes it from the more tur-
bulent habitats. However, *Justicia* is the dominant emergent plant in the New
River, contributing 12% of the aquatic macrophyte biomass (Hill 1981).

Mosses and liverworts are the dominant macrophytes in environments with
the highest turbulent flows (Westlake 1975). This situation may be partially
due to the fact that bryophytes are able to use free CO$_2$ as a carbon source
(Gessner 1959) and turbulent water insures CO$_2$ saturation. Messer et al.
(1986) and Kaufmann et al. (1988) reported that most small streams in the
southern Blue Ridge are probably supersaturated with respect to CO$_2$. Sub-
strate stability is probably another factor influencing local moss distribution,
since mosses tend to be most abundant on bedrock and large boulder sub-
surveyed the bryophyte flora of high-gradient Appalachian streams exten-
sively and found four bryophytes to dominate. *Fontinalis dalecarlica* is the
most ubiquitous aquatic moss, occurring in first- to third-order streams in
depths of 10–100 cm. The gametophyte typically forms mats with “stream-
ers”. *Hygroamblystegietum fluviatile* dominates relatively shallow, first- and
second-order streams, forming thick mats on submerged rocks, but may occur
as a subdominant in larger streams. The distribution of two other potentially
dominant bryophytes, *Sciaromium leucrillii* and *Scapania undulata*, is poorly
known (Glime 1968). An aquatic species of *Fissidens*, a largely terrestrial
moss genus, seems to occur in habitats with higher levels of NO$_3$ and PO$_4$ as
well as CO$_2$, such as Doe Run in Kentucky (Minckley 1963).

Algae

The algae of high-gradient streams are likewise limited to species that are
anchored to stable substrates. Attachment to large, stable objects is of prime
importance for the success of this group. Although an algal population may
expand to smaller rocks and pebbles during low flows, a spate that causes
stones to tumble may remove individuals from all but the largest stones
(Minckley and Tindall 1963). The algal flora of the high-gradient streams of
the southeastern United States is dominated by filamentous red algae (Rho-
dophyta), filamentous green algae (Chlorophyta), and diatoms (Bacillar-
iphyta), although other groups are represented in reduced numbers.

Many species of algae appear to be restricted to or at least maintain large
populations in this region. Two taxa of red algae, *Nemalionopsis shawii* f.
caroliniana and *Boldia erythrosiphon*, occur only in streams of the southeast
(Howard and Parker 1979, 1980). Camburn and Lowe (1978) described a new
diatom from high-gradient streams of the region (*Achnanthes subrostrata* v.
apalachiana) that comprised as much as 73% of the algal community in high-
gradient streams in the Great Smokies. There have been a limited number
of algal surveys of high-gradient streams of the southeastern United States
(Silva and Sharp 1944, Dillard 1969, 1971, Camburn et al. 1978, Lowe and
Kociolek 1984). Communities of microalgae are most often dominated by
diatoms with a high degree of substrate affinity. Species of *Achnanthes* and
*Eunotia*, and to a lesser extent *Meridon*, *Diatoma*, *Gomphonema*, and *Na-
vicula*, dominate the diatom communities of turbulent first- and second-order
streams in the southern Appalachian Mountains (Fig. 4a, b) (Kociolek 1982,
Keithan and Lowe 1985, Lowe et al. 1986). *Achnanthes* is a genus of tightly

![FIGURE 4. Scanning electron micrographs of epilithic periphyton from Camel Hump, Great Smoky Mountain National Park. (A) A, Achnanthes deflexa; E, Eunotia rhomboidea (at 1500 × magnification). (B) M, Meridon circulare (at 700 × magnification). (Photos supplied by Elaine Keithan.](image)
adhering diatoms that may be the most abundant diatom genus in swift streams of the Great Smoky Mountains. Kociolek (1982) observed 21 species of *Achnanthes* in the Smokies. In the two streams most carefully investigated by Kociolek, *Achnanthes* comprised 40–50% of the diatom community. The highly motile and planktonic genera that often dominate low-gradient streams (*Nitzschia*, *Suriella*, *Cyclotella*, and *Stephanodiscus*) are conspicuously sparse in high-gradient streams in the Smokies.

Whitford and Schumacher (1963) collected extensively in high-gradient streams in North Carolina, including the French Broad, New Watauga, Tuckasegee, Cullasaja, and Oconaluftee rivers. Their work provides excellent general information on algal distribution in these streams. The diatoms *Gomphonema parvulum* var. *subelliptica*, *Eunotia alpina*, and *E. lunaris*; the green algae *Oedogonium kurzii* and *Protoderma viride*; the red algae *Compsopogon coeruleus*, *Audouinella violacea*, *Batrachospermum boryanum*, *B. sirodotii*, *Lemania fucina*, and *L. australis*; the chrysophytes *Vaucheria ornithocephala* and *Phaeodermatiwn rivulare*; and the blue-green algae *Entophysalis lemanianae*, *E. rivularis* and *Phormidium subfuscum* were all recognized as lotic species by Whitford and Schumacher (1963) and were most abundant in swift rapids.

**Primary Production**

The rate of primary production in high-gradient streams varies with stream order, season, degree of shading, and nutrients. Hornick et al. (1981) estimated gross primary production (GPP as carbon) in a third-order hardwater stream in Virginia as 6.54 g C/m² year⁻¹ (or as ash free dry mass, ca. 14 g/m² year⁻¹). They found that GPP in unshaded sites was three times that of shaded stream sites. Keithan and Lowe (1985) found very similar rates of primary productivity (7–9 g C/m² year⁻¹) in two small streams in the Great Smoky Mountains. Primary production in a heavily shaded, second-order, softwater stream at Coweeta in western North Carolina was only 1.3 g C/m² year⁻¹ (= ca. 2.9 g AFDM/m² year⁻¹) (Webster et al. 1983). In contrast, that of a nearby stream draining a clear-cut catchment was 38.9 g C/m² year⁻¹ (= ca. 86.6 g AFDM/m² year⁻¹). However, within two years, rapid regrowth of riparian vegetation on the clear-cut catchment resulted in heavy shading, and primary production declined to 3.9 g C/m² year⁻¹ (= 8.8 g AFDM/m² year⁻¹) (Webster et al. 1983). In a later study comparing the same streams, periphyton biomass in the clear-cut stream was still higher than in the reference stream; however, in both streams periphyton biomass was unaffected by nutrient additions (Lowe et al 1986). Elwood and Nelson (1972) measured periphyton production with ³²P in Walker Branch, Tennessee, as 7.54 g AFDW/m² year⁻¹, about 2.6 times that found in a similar size softwater stream at Coweeta. Hill and Webster (1982b) found periphyton primary production values ranging from 9.3 to 1.059 mg C/m² day⁻¹ in the sixth-order, New River, Virginia, with production in the hardwater reaches exceeding that of the softwater.
reaches by 3–5 times. They attributed differences in production between reaches to greater dissolved inorganic carbon in the hardwater reaches of the river.

Macrophyte production has been studied in two reaches of the New River, Virginia (Hill and Webster 1983, Rodgers et al. 1983), and the Watauga River, Tennessee (Rodgers et al. 1983). In the upper portion of the New River, macrophytes contributed about 63.65 g AFDM/m² of river surface area a year to organic matter inputs of the river (Hill and Webster 1983). Macrophytes contributed about 13.1% of the total inputs to the upper reaches of this river. *Podostemum ceratophyllum* contributed about 80% of the total macrophyte inputs into the upper reaches of the New River, with smaller contributions by *Justicia americana* (12.5%) and *Typha latifolia* (6.8%), and minor contributions by *Potamogeton crispus* and *Elodea canadensis* (Hill and Webster 1983). However, in downstream reaches *Justicia americana* and *Typha latifolia* were found to contribute most macrophyte production (Rodgers et al. 1983). *Podostemum ceratophyllum* and *Nitella flexilis* were the most productive macrophytes in the Watauga River (Rodgers et al. 1983).

### Allochthonous Energy Sources

Allochthonous organic material, that is, direct litterfall and lateral movement of leaves and wood from riparian forests, is the predominant energy source in high-gradient streams of the southern Appalachians (e.g., Hornick et al. 1981, Webster et al. 1983). Forest litterfall in the region averages about 400 g dry mass/m² year⁻¹ (Bray and Gorham 1964), and this is probably a good estimate for direct litterfall inputs to headwater streams (Table 4). However, as stream width increases, direct litterfall decreases (e.g., Hornick et al. 1981, Connors and Naiman 1984). Lateral movement is highly variable, depending on such factors as wind patterns, aspect, and bank slope, and its relative contribution to stream inputs varies with stream width (Table 4). Wood generally comprises about 25% of the total input but may approach 50% (Table 5). Logging greatly reduces allochthonous inputs (Webster and Waide 1982), but inputs may be quantitatively near normal within 6–8 years after logging (Webster et al. 1990). However, qualitative differences in litter inputs may persist for many years following logging (Webster et al. 1983, Webster et al. 1990). Inputs from successional vegetation are generally more labile and decay more rapidly in the stream (Webster and Waide 1982, Webster et al. 1983, Benfield et al., 1991). In summary, allochthonous inputs of terrestrial organic matter represent a much larger energy input to small, undisturbed headwater streams of the Appalachians than autochthonous production.

Dissolved organic carbon (DOC) represents another potential energy source to stream ecosystems. External sources of DOC include groundwater inputs and throughfall, while instream sources include leaching from detritus stored in the stream bed as well as dissolved exudates from the biota. Leaching of DOC may be enhanced by microbial activity and macroinvertebrate feeding (Meyer and O'Hop 1983). At the two sites, Coweeta and Walker Branch,
TABLE 4  Litter Inputs to Undisturbed Southern Appalachian Streams.

<table>
<thead>
<tr>
<th>Stream</th>
<th>Average Stream Width (m)</th>
<th>Litterfall (g/m² year⁻¹)</th>
<th>Lateral movement (g/m² year⁻¹)</th>
<th>Ratio of Litterfall to Lateral Movement</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coweeta WS 7, NC</td>
<td>1.65</td>
<td>259</td>
<td>175</td>
<td>212</td>
</tr>
<tr>
<td>Walker Branch, TN</td>
<td>5.56</td>
<td>372</td>
<td>278</td>
<td>100</td>
</tr>
<tr>
<td>Guys Run, VA</td>
<td>—</td>
<td>347</td>
<td>—</td>
<td>113</td>
</tr>
<tr>
<td>Coweeta WS 14, NC</td>
<td>4.04</td>
<td>415</td>
<td>89</td>
<td>44</td>
</tr>
<tr>
<td>Coweeta WS 18, NC</td>
<td>1.24</td>
<td>482</td>
<td>136</td>
<td>220</td>
</tr>
</tbody>
</table>

**Note.** Lateral movement is given in both per unit length of stream and per m² of stream area. The ratio of litterfall to lateral movement is based on inputs per unit area of stream.

*Webster and Waide (1982).
*Comiskey et al. (1977).
*Hornick et al. (1981).
*Webster et al. (1990).
TABLE 5 Litter Inputs to Streams at Coweeta Hydrologic Laboratory

<table>
<thead>
<tr>
<th>Location</th>
<th>Litterfall (g/m² year⁻¹)</th>
<th>Lateral Movement (g/m year⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Leaf</td>
<td>Wood</td>
</tr>
<tr>
<td>Watershed 18 undisturbed, 1st order</td>
<td>482.2</td>
<td>259.7</td>
</tr>
<tr>
<td>Watershed 14 (undisturbed, 2d order)</td>
<td>415.4</td>
<td>90.9</td>
</tr>
<tr>
<td>Watershed 6 (successional, 1st order)</td>
<td>332.3</td>
<td>105.6</td>
</tr>
<tr>
<td>Watershed 7 (successional, 2d order)</td>
<td>354.2</td>
<td>33.9</td>
</tr>
</tbody>
</table>

Note. Lateral movement is based on input per linear meter of channel.
Source. From Webster et al. (1990).

where DOC has been studied extensively, concentrations of DOC are low (<1.5 mg/L) during base flow conditions (Meyer et al. 1988, Elwood and Turner 1989). At Walker Branch, concentrations of DOC in streamwater are comparable to those entering via the groundwater at base flow, which suggests either that stream concentrations mirror that of entering groundwater or that a steady state exists between groundwater and in-channel inputs (leaching and exudates) and in-channel uptake, adsorption, and oxidation (Elwood and Turner 1989). In contrast, at Coweeta there are increases in DOC concentration from seeps to downstreams reaches (Meyer and Tate 1983, Meyer et al. 1988, Wallace et al., unpublished). Leaching of organic matter in the stream bed with influence of biological activity appears to be the major source of this downstream increase in DOC (Meyer and O'Hop 1983, Meyer et al. 1988).

Role of Woody Debris

Most smaller first- through third-order streams have low stream power (Leopold et al. 1964), very high channel roughness (Chow 1959), and shallow, narrow channels that are easily obstructed. These features enhance the retention of coarse particulate organic matter (CPOM) such as woody debris and leaves within these channels (Sedell et al., 1978, Naiman and Sedell 1979a, Bilby and Likens 1980, Wallace et al. 1982a, Cummins et al. 1983, Minshall et al. 1983).

In these small headwater streams within forested regions, woody debris not only is a potential energy source, but also serves an important structural role (Swanson et al. 1982, Harmon et al. 1986). These types of streams are
common in New England (Bilby and Likens 1980), Oregon (Anderson and Sedell 1979, Naiman and Sedell 1979a, Triska and Cromack 1981, Speaker et al. 1984), the southern Rocky Mountains of New Mexico (Molles 1982), and the southern Appalachians (Wallace et al. 1982a, Webster and Swank 1985a, Golloday et al. 1987, 1989). Woody debris has many roles in high-gradient streams (Harmon et al. 1986), which include contributing to stair-step profiles that result in rapid dissipation of the stream’s energy (Bilby and Likens 1980); retention of other particulate organic matter (e.g., Bilby and Likens 1980, Molles 1982, Speaker et al. 1984, Golloday et al. 1987), which may influence both trophic and nutrient dynamics (e.g., Bilby 1981, Molles 1982, Newbold et al. 1982, Mellilo et al. 1983, Webster and Swank 1985a, Webster et al., 1990); providing fish habitat (Triska and Cromack 1981, Sedell et al. 1982); and providing a substrate for some stream invertebrates (Anderson et al. 1978), and food for some aquatic invertebrates that may be xylophagous (Anderson et al. 1978, Anderson and Sedell 1979, Dudley and Anderson 1982, Pereira et al. 1982).

**Organic Matter Processing**

Organic matter exported to downstream reaches consists primarily of fine particulate organic matter (FPOM) and dissolved organic matter (DOM) (Naiman and Sedell 1979b, Webster and Patten 1979, Wallace et al. 1982a, Minshall et al. 1983). Despite the large preponderance of CPOM inputs to small headwater streams at the Coweeta Hydrologic Laboratory in western North Carolina, about 80–95% of the particulate organic matter exported to downstream reaches consists of FPOM. Most of the CPOM export occurs during a few major storms during the year (Cuffney and Wallace 1989, Wallace et al., 1991). Therefore, these small headwater streams function as sites for storage, processing (CPOM to FPOM and DOM), and transport of organic matter (Cuffney et al. 1984, Wallace et al. 1986).

The FPOM and DOM exported from small headwater streams to downstream areas appears to comprise an important energy and nutrient source to downstream microbial flora and fauna. Those fauna adapted for deposit and filter feeding (Short and Maslin 1977, Anderson and Sedell 1979, Wallace and Merritt 1980) may be especially dependant on upstream sources of FPOM. Up to 96% of the annual FPOM flux through downstream segments may originate from upstream sources (Fisher 1977). This longitudinal upstream to downstream linkage has formed the basis for concepts such as nutrient spiraling (Webster and Patten 1979, Newbold et al. 1982) and the River Continuum Concept (Vannote et al. 1980, Minshall et al. 1983).

**ANIMAL COMMUNITIES**

The streams of the southern Appalachian region contain a diverse fauna of invertebrates, salamanders, and fish. High-gradient streams in the southern Appalachians, ranging from 300 to >2000 m above sea level, are subjected
ANIMAL COMMUNITIES

to very different thermal regimes. The wide array of temperatures, combined
with diverse stream chemistries, flow, and local geomorphology, influence
the species that constitute animal communities.

Invertebrates

The diversity of aquatic invertebrate species in the southern Appalachian
Mountains is probably greater than that of any region in North America (Holt
1969, Brigham et al. 1982). Holt (1969) suggested that the area represents
an important center for evolution and also an area with many endemic species.
This diverse fauna has been attributed to the long-term stability resulting from
little major geological change other than climatic trends and fluctuations since
the Cretaceous, some 63–135 million years ago (Holt 1969). In their com-
prehensive treatment of the aquatic insects and oligochaetes of North and
South Carolina, Brigham et al. (1982) acknowledged that their treatment of
the fauna was incomplete and suggested that for some groups, such as the
Chironomidae (Diptera), over 50% of the fauna remains undescribed.

The cool, high-elevation streams may contain taxa that are typical of nor-
thern climates and, therefore, do not occur elsewhere in the southeastern region.
Detailed systematic treatment of various groups of invertebrates is beyond
the scope and objectives of this chapter. Brigham et al. (1982), Merritt and
Cummins (1984), and Pennak (1978) should be consulted for general system-
atic references. We will stress a functional approach built around habitat,
trophic organization, and the functional role of invertebrates in streams to
bridge the diverse stream habitats of the southern Appalachians.

Cumins proposed a scheme of functional classification based on morpho-
behavioral mechanisms used to acquire food (Cummins 1973, Cummins and
Klug 1979, Merritt and Cummins 1984). These functional feeding groups are
as follows:

**Scrapers:** Animals adapted to graze or scrape materials (periphyton, or
attached algae, and its associated microflora) from mineral and organic
substrates.

**Shredders:** Organisms that chew primarily large pieces of decomposing
vascular plant tissue (>1 mm diameter) along with its associated mi-
croflora and fauna, feed directly on living vascular hydrophytes, or gouge
decomposing wood submerged in streams.

**Collector-gatherers:** Animals that feed primarily on fine pieces of decom-
posing particulate organic matter (FPOM = <1 mm diameter) deposited
within streams.

**Collector-filterers:** Animals that have specialized anatomical structures
(setae, mouthbrushes, fans, etc.) or silk and silk-like secretions that act
as sieves to remove particulate matter from suspension (Jorgensen 1966,
Wallace and Merritt 1980).

**Predators:** Those organisms that feed on animal tissue by either engulfing
their prey or piercing prey and sucking body contents.
These functional feeding groups refer primarily to modes of feeding and not type of food per se. For example, many filter-feeding insects of high-gradient streams are primarily carnivores (Benke and Wallace 1980). Scrapers also consume quantities of what must be characterized as epilithon (Lock 1981) and not solely periphytic algae. Likewise, although shredders may select those leaves that have been "microbially conditioned" by colonizing fungi and bacteria (e.g., Cummins and Klug 1979), they also ingest attached algal cells, protozoans, and various other components of the meiofauna during feeding (Merritt and Cummins 1984). Some shredders apparently obtain very little of their assimilated energy directly from microbial biomass (Cummins and Klug 1979, Findlay et al. 1984), although microbially derived enzymes from endosymbionts or enzymes obtained from microbes ingested with leaf tissue may be important in cellulose hydrolysis (Sinsabaugh, et al. 1985). While it appears valid to separate taxa according to the mechanisms used to obtain foods, many questions remain concerning the sources of protein, carbohydrates, fats, and assimilated energy to each of these functional groups.

A major problem faced by invertebrates in high-gradient streams is maintaining their position in areas of high current velocity. Many taxa have evolved rather elaborate morphological and behavioral adaptations for maintaining their position in such microhabitats (see Hynes 1970, Merritt and Cummins 1984).

Scrapers Scrapers in high-gradient southeastern streams include a rather diverse assemblage of taxa (Table 6). In small woodland streams draining areas of the crystalline rock, scraper production appears to be limited by levels of primary production (e.g., Wallace and Gurtz 1986). Some scrapers, for example, Goerita semata Ross (Trichoptera: Limnephilidae), have two-year life cycles in heavily shaded, high-elevation streams. Seasonal differences in larval growth rates of G. semata suggest that these are closely linked to seasonal levels of primary production and temperature regimes (Huryn and Wallace 1985). Even in the open, fourth-order, sunlit streams of the Blue Ridge, invertebrate scrapers show considerable temporal segregation in secondary production, and the seasonal distribution of secondary production correlates well with that reported for seasonal changes in periphyton production (Georgian and Wallace 1983). To date, no study has compared seasonal estimates of periphyton production, scraper production, and their biochemical efficiencies to estimate the proportion of periphyton production utilized by the scraper guild. Lamberti and Moore (1984) summarized the ecological roles proposed for scrapers, or grazers, in stream ecosystems.

Shredders In areas dominated by crystalline rocks, the predominant shredders in the southern Appalachians include crayfish and aquatic insects (Table 6). Feeding of macroinvertebrates on CPOM, or "shredding," increases at the rate which CPOM is converted to FPOM (Cummins 1973, Petersen and Cummins 1974). Shredder feeding also enhances the conversion of CPOM to dissolved organic matter (Meyer and O'Hop 1983). The generation of large...
<table>
<thead>
<tr>
<th>Functional Feeding Group</th>
<th>Dominant Groups</th>
<th>Dominant Families</th>
</tr>
</thead>
<tbody>
<tr>
<td>Scrapers</td>
<td>Trichoptera</td>
<td>Baetidae, Ephemereillidae, and Leptophlebiidae</td>
</tr>
<tr>
<td></td>
<td>Plecoptera</td>
<td>Glossosomatidae, Brachycentridae, and Limnephilidae</td>
</tr>
<tr>
<td></td>
<td>Coleoptera</td>
<td>Psephenidae and Elmidae</td>
</tr>
<tr>
<td></td>
<td>Diptera</td>
<td>Blephariceridae, Thaumaleidae, and Chironomidae</td>
</tr>
<tr>
<td></td>
<td>Gastropoda</td>
<td></td>
</tr>
<tr>
<td>Shredders</td>
<td>Trichoptera</td>
<td>Pteronarcyidae, Peloperlidae, Nemouridae, and Leuctridae, and Capniidae</td>
</tr>
<tr>
<td></td>
<td>Plecoptera</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Diptera</td>
<td>Lepidostomatidae, Limnephilidae, and Sericostomatidae</td>
</tr>
<tr>
<td></td>
<td>gastropoda</td>
<td></td>
</tr>
<tr>
<td>Collector-gatherers</td>
<td>Oligochaeta (most) and Collembola</td>
<td>Hepageniidae, Ephemereillidae, and Leptophlebiidae</td>
</tr>
<tr>
<td></td>
<td>Plecoptera</td>
<td>Taenioperygidae and Nemouridae</td>
</tr>
<tr>
<td></td>
<td>Coleoptera</td>
<td>Elmidae</td>
</tr>
<tr>
<td></td>
<td>Diptera</td>
<td>Psychodidae, Dixa, Tipulidae, and Chironomidae</td>
</tr>
<tr>
<td></td>
<td>Crustacea</td>
<td>Copepoda, Ostracoda, Isopoda, and Amphipoda</td>
</tr>
<tr>
<td></td>
<td>mollusca</td>
<td>Gastropoda</td>
</tr>
<tr>
<td>Collector-filterers</td>
<td>Plecoptera</td>
<td>Some Oligoneuridae</td>
</tr>
<tr>
<td></td>
<td>Trichoptera</td>
<td>Philoptamidae, Hydropsychidae, and Brachycentridae</td>
</tr>
<tr>
<td></td>
<td>Diptera</td>
<td>Simulidae, Dixa, and Chironomidae</td>
</tr>
<tr>
<td></td>
<td>Mollusca</td>
<td>Sphaeridae and Pelecypoda</td>
</tr>
<tr>
<td>Predators</td>
<td>Turbellaria, Nematoda, and Odonata</td>
<td>Periidae, Perlididae, and Chloroperlidae</td>
</tr>
<tr>
<td></td>
<td>Plecoptera</td>
<td>Corydalidae and Sialidae</td>
</tr>
<tr>
<td></td>
<td>Megaloptera</td>
<td>Rhyacophilidae, Molannidae, Leptoceridae and several filtering-collector taxa exploit invertebrate drift</td>
</tr>
<tr>
<td></td>
<td>Trichoptera</td>
<td>Tipulidae, Chironomidae, Ceratopogonidae, Tabanidae, Athericidae, Dolichopodidae, Empididae, and Muscidae</td>
</tr>
<tr>
<td></td>
<td>Diptera</td>
<td>Some Decapoda</td>
</tr>
</tbody>
</table>

Note. For detail listing of various genera, consult works such as those of Pennak (1978), Brigham et al. (1982), and Merritt and Cummins (1984).
quantities of small particles, which are more amenable to downstream transport and increase the surface area for microbial colonization, is probably far more important than the shredders' ability to directly degrade organic material by metabolic respiration. Direct metabolic respiration by invertebrate fauna in Bear Brook, New Hampshire, was considered to represent <1% of the annual flux of organic matter through the stream (Fisher and Likens 1973). However, when feeding activities, bioenergetic efficiencies, and secondary production of invertebrates were considered, their overall impact on detritus processing was much greater than 1% in a second-order southern Appalachian stream (Webster 1983). Webster's (1983) model estimated that shredders were responsible for 13% of the leaf litter processing and macroinvertebrates accounted for 27% of the annual particulate organic matter (POM) transport.

Despite the indirect evidence for the role of shredders in processing organic matter in headwater streams there has been little direct evidence to quantify the importance of shredders (Merritt et al. 1984). In a retentive southern Appalachian headwater stream in western North Carolina, the application of an insecticide resulted in massive invertebrate drift and subsequent changes in community structure that eliminated >90% of the insect density and biomass. Elimination of the aquatic insects significantly reduced leaf litter processing rates and export to FPOM to downstream reaches compared to an adjacent, untreated, reference stream (Wallace et al. 1982b, Cuffney et al. 1984). Furthermore, restoration of shredder functional group biomass coincided with restoration of leaf litter processing rates and FPOM export in the treated stream (Wallace et al. 1986). A more recent and expanded experimental manipulation of macroinvertebrate populations in another headwater stream at Coweeta showed that macroinvertebrates accounted for 25 to 28% of annual leaf litter processing (Cuffney et al. 1990) and 65% of the annual FPOM export (Cuffney and Wallace 1989).

Thus, biological processes in small, high-gradient streams, where there is high physical retention of CPOM inputs, favor entrainment by processing CPOM to smaller particles (FPOM) that are more amenable to transport than CPOM (Wallace et al. 1982b, Cuffney et al. 1984). The biota may play a significant role in the upstream to downstream linkage although the instream biota represent a small fraction of total watershed biomass. The above studies were conducted in small first-order streams in the Blue Ridge province and the extent to which these studies apply to larger streams and/or other geographical areas has not been assessed.

**Collector-Gatherers** Collector-gatherers are adapted to feeding primarily on small particles (<1 mm diameter) that are deposited on substrate surfaces or in depositional areas of streams. Some typical examples of collector-gatherers found in Appalachian streams are given in Table 6.

The functional role of collector-gatherer invertebrates in high-gradient streams of the Southeast has not been studied directly. Fisher and Gray (1983) provided an excellent account of the role of the collector-gatherers in Sycamore Creek, Arizona. While assimilation efficiencies were low (7–15%),
the animals had high ingestion rates in this stream and consumed food equivalent to their own body weight every 4–6 h. Fisher and Gray suggested that egested feces (lower food quality) were rapidly colonized by microbes, which were reingested every 2–3 days on the average. Although growth rates of some collector–gatherers, such as Chironomidae, may be surprisingly high, even in cool, high-elevation Appalachian streams (Huryn and Wallace 1986, Huryn 1990), they are not nearly as rapid as those found in the warm water stream studied by Fisher and Gray (1983). Many of the collector–gatherers in Table 6 contribute to similar processes of FPOM turnover in Appalachian streams. For example, collector-gatherer chironomids alone may consume and egest a large portion of the FPOM stored in headwater Appalachian streams (Schurr and Wallace, unpublished data).

Collector–Filterers There is extensive literature on filter-feeding insects (see Wallace and Merritt 1980, Merritt and Wallace 1981) and other invertebrate filter feeders (Jorgensen 1966, 1975). The animals listed in Table 6 constitute a heterogenous group with respect to feeding, since many of the Hydropsychidae and Brachycentridae (Trichoptera) rely primarily on animal drift (Wallace et al. 1977, Benke and Wallace 1980, Georgian and Wallace 1981, Ross and Wallace 1981, 1983). Although these animals may be filter feeders based on their mode of food capture, they may also be carnivorous, while some taxa, such as Philopotamidae, Simulidae, Chironomidae (Wallace and Merritt 1980, Merritt and Wallace 1981), and Sphaeriidae (Pennak 1978), exploit minute particles suspended in the water column. With the exception of Brachycentridae, larvae of Trichoptera use a diverse assemblage of woven silken nets to capture particles. Individual pore or mesh sizes of catchnets of various taxa range from <1 μm to 500 × 500 μm. Larger catchnet mesh sizes, such as found within the Arctopsychinae (Hydropsychidae), are located primarily in high-velocity microhabitats, such as swift, moss-covered, rock-face habitats (Gurtz and Wallace 1986, Smith-Cuffney and Wallace 1987, Huryn and Wallace 1987), whereas those with minute mesh openings, such as Philopotamidae, are located in microhabitats of low velocity, for example, on undersides of stones (Wallace et al. 1977, Malas and Wallace, 1977, Georgian and Wallace 1981). Some filter feeders, such as the Philopotamidae and the Simulidae, may actually increase particle sizes by ingesting minute FPOM and egesting compacted fecal particles larger than those originally consumed (Wallace and Malas 1976). Thus, these animals may perform two very important functions: (1) They remove very fine particulate organic matter from suspension (which would otherwise pass through the stream segment), and (2) they defecate larger particles, which are available to a broad spectrum of larger-particle-feeding detritivores.

Studies conducted in high-gradient streams of the Southeast indicate that filter feeders remove a minute fraction of the total particulate organic matter in transport and that their major impact appears to be on seston quality rather than quantity (Benke and Wallace 1980, Georgian and Wallace 1981, Haefner and Wallace 1981a, Ross and Wallace 1983). Newbold et al. (1982) suggested
ALACHIANS

ream probably far nic material brate fauna <1% of the kens 1973). A secondary on detritus Appalachian edders were tebrates ac- ) transport. sing organic to quantify ve southern aplication of ent changes ity, and bio- if litter prepared to an ifney et al. omass coin- xport in the ded experi- r headwater r 25 to 28% the annual ere there is processing nspor than may play a he instream ove studies rovince and other geo-

that filter-feeders may shorten nutrient spiralling length when particulate transport is high and there is strong nutrient limitation. However, when there is a high rate of nutrient regeneration, filter feeders probably have little influence on spiralling length.

**Predators** Invertebrate predators commonly inhabiting high-gradient streams include several Turbellaria, some Nematoda, Hydracarina, several groups of insects, and some crayfish (Table 6). Brigham et al. (1982) and Merritt and Cummins (1984) should be consulted for specific taxa of aquatic insect predators within the region. Allan (1983) and Peckarsky (1984) reviewed the literature associated with predator-prey relationships in streams. Although there is some experimental evidence that predators can influence the structure of lentic and intertidal communities, there is no strong evidence for predators significantly influencing lotic community structure (Allan 1983). Allan suggested several reasons why benthic communities of streams are not structured by predation. These include the absence of a dominant predator, the presence of many refuges, cryptic coloration, and behavioral adaptations of prey. Another reason that it may be hard to show significant influences on invertebrate community structure as a consequence of predation may be that, on the average, prey standing stock biomass and the generation time of many prey far exceed that of their invertebrate predators in most high-gradient streams of the Southeast. The majority of invertebrate predators have slow growth rates, uni- or semivoltine life cycles and rather low annual production to standing stock biomass ratios ($P/B \leq 5$). In addition, these predators generally represent less than 20% of the total invertebrate standing stock biomass, whereas nonpredators comprise over 80% of total biomass and have life cycles that range from a few weeks (e.g., Chironomidae) to a year, with annual $P/B$'s ranging from 5 to $>40$ (see Production section below). Thus, it is difficult to envision that predators, with high bioenergetic efficiencies (e.g., Lawton 1970, Brown and Fitzpatrick 1978), long life cycles, slow growth rates, and hence, slow population response times, would produce immediate and substantial effects on lotic community structure. Heterogenous substrates, which may provide refuges for benthic prey (Allan 1983), and the selection of a broad spectrum of prey taxa by individual invertebrate predators would further dampen the direct effects of predation in these small headwater streams.

Data on prey and predator production, the relative availability of prey production to predators, and the bioenergetics of predators are required before making any definitive conclusions about the influence of predation on lotic communities. Assessments of predator-prey relationships based on either numerical abundances or biomass are tenuous.

**Longitudinal and Mesospatial Distributions** Streams display continuous changes in physical and chemical characteristics from headwaters to mouth, which may influence the structure and function of biological communities along this continuum (Vannote et al. 1980). Changes along this continuum may be interrupted or discontinuous due to changes in hydrodynamic characteristics.
ANIMAL COMMUNITIES

(Statzner and Higler 1985). From headwaters to mouth, streams display longitudinal shifts in many attributes, including (1) the relative proportion of allochthonous and autochthonous (instream primary production) organic matter contributions; (2) the relative importance of organic matter inputs from upstream sources; (3) longitudinal changes in physical characteristics such as retention; and (4) discharge and thermal regimes. These characteristics play an important role in the relative distribution of stream animals that are adapted to utilize various food resources (Vannote et al. 1980). Furthermore, differences in current velocity and retention characteristics may occur over short reaches. Too often biologists fail to recognize that very localized differences in stream geomorphology result in extremely strong influences on benthic community structure. For example, Brussock et al. (1985) discussed the importance of considering channel form in stream ecosystem models.

Secondary Production of Invertebrates

Benke (1984) defined secondary production as "the living organic matter, or biomass, produced by an animal population during an interval of time." Secondary production is thus a measure of the rate at which animal biomass is produced, regardless of its fate (e.g., loss to predators, natural mortality, emergence), and its units are biomass or energy per unit area, per unit time. Most studies of secondary production in stream ecosystems have been limited to a few taxa within a given stream, and there have been few studies that assessed secondary production of the entire macroinvertebrate community within a stream. Secondary production estimates require a knowledge of life cycles or specific growth rates, standing stock densities, and biomass. Thus, such studies are labor intensive. Voltinism and length of immature development have been identified as the two most important factors influencing secondary production of aquatic invertebrates (Benke 1979, Waters 1979). The integration of production, feeding habits, and bioenergetic data can yield a much better understanding of the role of animal populations in ecosystems than either abundances or standing stock biomass (Benke and Wallace 1980, Fisher and Gray 1983, Webster 1983, Benke 1984).

To date, most secondary production studies of invertebrates in high-gradient streams have focused on bivoltine, univoltine, or semivoltine species with clearly discernable life cycles. In some cases, shortcut methods, such as estimating secondary production as the product of standing crop biomass and some production/biomass (P/B) ratio (usually 3.5 to 5; Waters 1977), have been used. The estimates listed in Table 7 include only examples where secondary production was actually measured, and not those based on assumed P/B ratios.

The study of Huryn and Wallace (1987a) adequately assessed secondary production of the entire invertebrate community in high-gradient streams of the Southeast and, to our knowledge, is the only such study for any high-gradient stream. In upper Ball Creek, a high-elevation (1035–1188 m a.s.l.) stream in western North Carolina, total secondary production of invertebrates was about 7.1 g ash free dry mass/m² year⁻¹ (Fig. 5a–d and Table 8) (Huryń and Wallace 1987a, b).
TABLE 7 Secondary Production of Aquatic Invertebrates in Some Southern Appalachian Streams

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Species/Names</th>
<th>Production (mg AFDM/m²/year)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Copepoda</td>
<td>Bryocamptus zschokkei [a]</td>
<td>P = ca. 360, NC</td>
</tr>
<tr>
<td>Ephemeroptera</td>
<td>Baetis spp. [b, c, e]</td>
<td>P = 15–1,112², NC, VA, WV;</td>
</tr>
<tr>
<td></td>
<td>Ephemerella [c]</td>
<td>P = 20–71, VA; Seratella sp. [d]</td>
</tr>
<tr>
<td></td>
<td>Heterocloeon curiosum [e]</td>
<td>P = 540, WV; Isonychia sp. [c, d]</td>
</tr>
<tr>
<td></td>
<td>Stenonema sp. [c, d]</td>
<td>P = 34–205, NC, VA</td>
</tr>
<tr>
<td>Odonata</td>
<td>Lanthus [c, d]</td>
<td>P = 6–53, NC, VA</td>
</tr>
<tr>
<td></td>
<td>Amphinemura sp. [d]</td>
<td>P = 14–130, NC; Leuctra spp. [d]</td>
</tr>
<tr>
<td></td>
<td>Peltoprionidae [d, f]</td>
<td>P = 32–560, NC; Pteronarcys [c]</td>
</tr>
<tr>
<td></td>
<td>Sweltsa spp. [d, g]</td>
<td>P = 20–142, NC, TN; Acroneuria [c]</td>
</tr>
<tr>
<td></td>
<td>Isoperla spp. [d]</td>
<td>P = 24–159, NC</td>
</tr>
<tr>
<td>Megaloptera</td>
<td>Nigronia [c]</td>
<td>P = 13–87, VA</td>
</tr>
<tr>
<td>Trichoptera</td>
<td>Rhyacophila spp. [d, h]</td>
<td>P = 2–211², NC; Wormaldia sp. [d, i]</td>
</tr>
<tr>
<td></td>
<td>Parapsychidae modesta [d, g, j, k, l]</td>
<td>P = 2–647, GA, NC, TN;</td>
</tr>
<tr>
<td></td>
<td>Parapsychidae cardis [d, j, k, l]</td>
<td>P = 33–4,274, GA, NC; Arctopsyche irrorata [j]</td>
</tr>
<tr>
<td></td>
<td>Cheumatopsyche spp. [i, e]</td>
<td>P = 26–84,654, NC, WV; Glossosoma sp. [l]</td>
</tr>
<tr>
<td></td>
<td>Trichoptera spp. [d]</td>
<td>P = 20–142, NC, TN; Acroneuria [c]</td>
</tr>
<tr>
<td></td>
<td>Isoperla spp. [d]</td>
<td>P = 24–159, NC</td>
</tr>
<tr>
<td>Coleoptera</td>
<td>Psephenus [d, e]</td>
<td>P = 15–180, NC, VA; Elmidae [c, d]</td>
</tr>
<tr>
<td></td>
<td>Decapoda</td>
<td>Cambarus spp. [c, p]</td>
</tr>
<tr>
<td></td>
<td>Mollusca</td>
<td>Leptoxis carinata [c]</td>
</tr>
</tbody>
</table>

Note. All values are in mg AFDM/m² year⁻¹. Those values initially reported as dry weight have been converted to AFDM based on a 15% ash content for insects and 30% for crayfish. Wet weight values were converted to AFDM based on 20% of wet weight. Following each taxon, references listed by letters in brackets refer to those listed at the bottom of the table. P, production, or range of production measured; localities are listed by state. This table is not complete. For production of additional taxa, consult the references listed below.

**References a–m as follows:**
- a = O'Doherty (1985);
- b = Wallace and Gurtz (1986);
- c = Miller (1985);
- d = Huryn and Wallace, 1987a;
- e = Voshell (1985);
- f = O'Hop et al. (1984);
- g = Cushman et al. (1977);
- h = D. H. Ross and J. B. Wallace (unpublished data);
- i = Ross and Wallace (1983);
- j = Benke and Wallace (1980);
- k = Haefner and Wallace (1981b);
- l = Georgian and Wallace (1983);
- m = Huryn and Wallace (1985);
- n = Ross and Wallace (1981);
- o = Lughart et al. in press; and, p = Huryn and Wallace 1987b.

1weighted stream production for all substrates for 21 month period.
2range for individual species (n = 5–6 species).
3range for individual species (n = 4 species).
4total production for 3 species.
Vertebrates

Two groups of communities occupy small streams primarily because they utilize the high favorable environment.

Salamanders

Desmognathus natalis marm, uncommon especially in the very large streams primarily because of the area. The salamander; an aquatics salamander stream distribution has been widely determined by Tilley and Erland 1986. small salamander has been widespread in the area.

Spight (1980) 0.4–1.4 ind 1.4 g of the total production in upper Ball Creek. Collector–gatherers contributed 51% to total primary consumer production and shredders 26%.

Figures 5a–d also shows the importance of considering substrate and stream geomorphology in assessing secondary productivity of high-gradient streams in the southern Appalachians. Within a given stream reach, distinct differences exist in functional group production for different types of substrates. The physical characteristics of these meso-spatial habitats influence resource availability and mode of resource availability to invertebrate consumers (Huryn and Wallace 1987a, 1988). Within the retentive pool habitats, collector–gatherers and shredders dominated invertebrate production, whereas collector–filterer production was largely restricted to the high-entrainment, low-retention, moss-covered rock face. In the rock-face habitat, moss also facilitates the retention of some fine particulate organic matter for collector–gatherers (see also Lugthart et al. 1990). Therefore, smaller meso-spatial

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and Wallace 1987a). Primary consumers (collector–gatherers, collector–filterers, shredders, and scrapers) contributed 5.7 g, and engulfing predators about 1.4 g of the total production in upper Ball Creek. Collector–gatherers contributed 51% to total primary consumer production and shredders 26%.

Figures 5a–d also shows the importance of considering substrate and stream geomorphology in assessing secondary productivity of high-gradient streams in the southern Appalachians. Within a given stream reach, distinct differences exist in functional group production for different types of substrates. The physical characteristics of these meso-spatial habitats influence resource availability and mode of resource availability to invertebrate consumers (Huryn and Wallace 1987a, 1988). Within the retentive pool habitats, collector–gatherers and shredders dominated invertebrate production, whereas collector–filterer production was largely restricted to the high-entrainment, low-retention, moss-covered rock face. In the rock-face habitat, moss also facilitates the retention of some fine particulate organic matter for collector–gatherers (see also Lugthart et al. 1990). Therefore, smaller meso-spatial

FIGURE 5. Comparison of some habitat characteristics with production of macroinvertebrate functional groups in Upper Ball Creek (WS 27) at the Coweeta Hydrological Laboratory in western North Carolina. (A) Moss, water velocity, and substrate particle size as measured for bedrock outcrops, riffles, and pools. (B) Average standing crops of fine particulate organic matter (FPOM), coarse particulate organic matter (CPOM) exclusive of wood, and small woody debris. (C) Secondary production for collector–filterer and scraper functional feeding groups. (D) Secondary production for collector–gatherer, shredder, and predator functional feeding groups. (Data from Huryn and Wallace 1987a, 1988.)
reaches occur within headwater streams which have physical characteristics that resemble various sites of the river continuum of Vannote et al. (1980). In turn, functional group production within specific meso-spatial reaches corresponds to that predicted for various reaches of the entire river continuum (Huryn and Wallace 1987a, 1988).

Chemical characteristics have a pronounced influence on gastropod abundances and production in southern Appalachian streams. At five sites along Guys Run, Virginia, secondary production of invertebrates ranged from 1.8 to 12.5 g DW/m² year⁻¹. Those stations in Guys Run with higher pH and hardness generally had the highest production, most of which was attributable to gastropods (Miller 1985). There was no gastropod production in upper, softwater reaches. However, some of the functional group placements, for example, crayfish as 100% predators and gastropods as 100% scrapers in Miller’s study are questionable (cf. Elwood et al. 1981, Huryn and Wallace 1987b). The annual $P/B$ ratios of the entire invertebrate community at the two softwater sites studied by Miller also seem to be very low (1.3 and 1.6) compared to those of a cooler softwater stream in western North Carolina (cf. Huryn 1986). Despite the questionable functional group assignments and $P/B$ ratios, the Guys Run study indicates the importance of chemical parameters in gastropod abundance and production. For example, in Walker Branch, Tennessee, a hardwater stream that drains a dolomite watershed, Goniobasis clavaeformis, a grazer-shredder, constitutes >95% of the macroinvertebrate biomass (Elwood et al. 1981) whereas at Coweeta in the crystalline Appalachian region of western North Carolina, snails are rare.

In contrast to the low invertebrate secondary production of headwater streams in the Appalachians, some extremely high, habitat-specific production

### TABLE 8

Annual Substrate-Specific and Substrate-Weighted (based on proportion of substrate types available) Macroinvertebrate Production, by Functional Feeding Group, Measured in Upper Ball Creek (Watershed 27) at the Coweeta Hydrologic Laboratory, Macon County, North Carolina

<table>
<thead>
<tr>
<th>Substrate Type</th>
<th>Collector-gatherer</th>
<th>Collector-filterer</th>
<th>Shredder</th>
<th>Scraper</th>
<th>Engulfing-predator</th>
<th>Total production</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rock Face</td>
<td>2.03</td>
<td>1.92</td>
<td>0.58</td>
<td>0.52</td>
<td>0.69</td>
<td>5.74</td>
</tr>
<tr>
<td>Cobble Ripple</td>
<td>2.64</td>
<td>0.28</td>
<td>1.66</td>
<td>0.91</td>
<td>1.38</td>
<td>6.87</td>
</tr>
<tr>
<td>Pool</td>
<td>4.05</td>
<td>0.03</td>
<td>2.62</td>
<td>0.24</td>
<td>2.23</td>
<td>9.17</td>
</tr>
</tbody>
</table>

Substrate-weighted (stream average)

- Collector-gatherer: 2.93
- Collector-filterer: 0.57
- Shredder: 1.48
- Scraper: 0.68
- Engulfing-predator: 1.40
- Total production: 7.06

**Note.** Rock face substrates = outcrops bedrock with attached moss, cobble riffles = primarily cobble and pebble (16 - to 256-mm-diameter particles), and pools = areas upstreams of debris dams. All values are in g AFDM/m² year⁻¹ and macroinvertebrates consist of all animals retained by a 230-µm mesh.

**Source.** From Huryn and Wallace (1987a).
has been reported for Appalachian rivers. On the Podostemum-covered, rock outcrop substrates in the New River below Bluestone Dam, West Virginia, Voshell (1985) estimated secondary production of invertebrates as 427.6 g dry mass/m² year⁻¹. This appears to be among the highest secondary production known for any stream. The high production is attributable primarily to chironomids and filter-feeding hydropsychid caddisflies and blackflies, which utilize the high-quality seston in the outflow from the reservoir within the favorable environment created by the thick Podostemum mat (Table 7) (Voshell 1985).

Vertebrates

Two groups of vertebrates are significant components of high-gradient stream communities of the Southeast: fish and salamanders. Salamanders usually occupy small headwater streams, and fish are found farther downstream. There is seldom much overlap in the distribution of these two groups, though the very large hellbender (Cryptobranchus alleganiensis) occurs in large clear streams primarily in the Mississippi drainage (Martof et al. 1980). Salamanders are generally restricted to small streams or the banks of larger streams, probably because of predation by fish.

Salamanders The most common stream salamanders belong to the genus Desmognathus (Plethodontidae), though shovel-nosed salamanders (Leurognathus marmoratus) and two-lined salamanders (Eurycea bislineata) are not uncommon in some streams, and other species may occasionally be found especially in spring seeps. Members of the genus Desmognathus range from aquatic to terrestrial. From 3 to 5 species are found in most areas of the southern Appalachian Mountains (Hairston 1986). The most common species are D. quadramaculatus, the black-belly salamander; D. monticola, seal salamander; and D. ochrophaeus, mountain dusky salamander. Desmognathus quadramaculatus is the largest and the most aquatic of the three, D. ochrophaeus is the smallest and most terrestrial, and D. monticola is intermediate (Hairston 1986). Other species of Desmognathus may occur in streams in part of the area (e.g., Martof et al. 1980).

Interspecific interactions of this group of Desmognathus salamanders have been widely studied (Hairston 1949, 1980, 1981, 1983, 1986, 1987, Organ 1961, Tilley 1968, Krzysik 1979, Keen 1979, 1982, Kleeberger 1984, Southernland 1986a,b). Competition for prey and predation of large salamanders on small salamanders appear to be the major factors determining the within-stream distribution of species. The role of salamanders in stream ecosystems has been much less studied, primarily because of difficulties of accurately determining population abundance and of identifying immature forms.

Spight (1967) estimated a stream population of Desmognathus fuscus of 0.4–1.4 individuals/m² in a North Carolina Piedmont stream. Using a mean
weight of 1.05 g/individual (based on his data), this converts to 0.4–1.5 g/m² standing stock. Spight also calculated production of this species of 0.1–0.3 g/m² year⁻¹ (Table 9). The resultant P/B of 0.2 seems low compared to fish (e.g., Neves and Pardue 1983). Orser and Shure (1972) found densities of *D. fuscus* varying from 0 to 10 individuals/m² in small streams near Atlanta, Georgia, using mark/recapture techniques. Based on Surber samples, Woodall (1972) estimated standing crop of *Desmognathus* salamanders (probably primarily *D. monticola*) in a small stream at Coweeta Hydrologic Laboratory in the southern Appalachians as 0.3 g/m². In the same stream, Drumheller (1979) used a census method to estimate salamander biomass and found a much lower density but a higher biomass (0.8 g/m²), since he collected fewer but larger individuals. For various first- to third-order streams in the area, Drumheller found that *Desmognathus* biomass ranged from 0.16 to 0.77 g/m² and production ranged from 0.20 to 1.16 g/m² year⁻¹. Production and biomass were both greater in first-order than in third-order streams. Drumheller's P/B ratios ranged from 1.5 to 1.8 for *D. quadramaculatus* and *D. ochrophaeus*, and from 0.9 to 1.0 for *D. monticola*. Huryn and Wallace (1987a) report P/B ratios of *Desmognathus* spp. ranging from 1.9 to 2.7. These P/B ratios are similar to or slightly greater than values usually reported for fish.

Stream salamanders are entirely predaceous and feed largely on terrestrial insects. Drumheller (1979) and others have shown that *Desmognathus* salamanders are size-selective predators, with larger salamanders consuming larger prey. Hairston (1949) reported that *D. quadramaculatus* stomachs contained 65%, *D. monticola* 75%, and *D. ochrophaeus* 100% terrestrial insects. Krzysik (1979) found that adult and larval dipterans were the primary food items of *Desmognathus* salamanders. Lepidoptera larvae, Coleoptera adults, and Plecoptera (adults and nymphs) were also important. More aquatic species consumed a larger proportion of aquatic insects, while more terrestrial species fed extensively on terrestrial invertebrates. In their examination of *Desmognathus* salamander gut contents, W. R. Woodall and J. B. Wallace (unpublished data) found that 54% of the food of adults was terrestrial, primarily Collembola and Hymenoptera. Overall, larval Diptera, primarily Chironomidae, were the most abundant aquatic food items for adult salamanders. Immature salamanders were found to feed much more extensively on aquatic insects.

### Table 9. Salamander Abundance, Biomass, and Production in Southeastern Headwater Streams

<table>
<thead>
<tr>
<th>Species</th>
<th>Abundances (No./m²)</th>
<th>Biomass (g/m²)</th>
<th>Production (g/m² year⁻¹)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>D. fuscus</em></td>
<td>0.4–1.4</td>
<td>0.4–1.5</td>
<td>0.1–0.3</td>
<td>Spight (1967)</td>
</tr>
<tr>
<td><em>D. fuscus</em></td>
<td>0–10</td>
<td>—</td>
<td>—</td>
<td>Orser and Shure (1972)</td>
</tr>
<tr>
<td><em>D. spp.</em></td>
<td>—</td>
<td>0.3</td>
<td>—</td>
<td>Woodall (1972)</td>
</tr>
<tr>
<td><em>D. spp.</em></td>
<td>—</td>
<td>0.16–0.77</td>
<td>0.20–1.16</td>
<td>Drumheller (1979)</td>
</tr>
<tr>
<td><em>D. spp.</em></td>
<td>2.7</td>
<td>0.113</td>
<td>0.242</td>
<td>Huryn and Wallace (1987a)</td>
</tr>
</tbody>
</table>
organisms: 96% of the food items in immature guts was aquatic. In forest streams gut content composition and composition of the benthic fauna were closely correlated, suggesting that salamanders are opportunistic feeders.

**Fish** Fish communities of high-gradient Southeastern streams may contain a variety of species (Table 10), but are usually dominated by trout, particularly brook trout (*Salvelinus fontinalis*). There has been little research on species other than trout beyond systematic and zoogeographical studies. There is a distinct zonation of fish species, which can be seen either by sampling along specific streams (e.g., Burton and Odum 1945; Neves and Pardue 1983) or by sampling many streams at different elevations (e.g., Harshbarger, in preparation). This zonation is reflected in species occurrence, biomass, and production (Tables 11 and 12). As noted above, fish are absent from the headwaters of streams. In this shallow water, salamanders are essentially the ecological equivalent of fish. Brook trout are the first to enter. Farther downstream they are joined by sculpins (*Cottus bairdi*), dace (e.g., *Rhinichthys atratus*), darters (e.g., *Etheostoma fiabellare*), and perhaps introduced rainbow (*Oncorhynchus mykiss*) and brown (*S. trutta*) trout. Proceeding downstream, other dace, darters, chubs, shiners, suckers, and other fish are found (Table 11). In larger downstream reaches smallmouth bass *Micropterus d. dolomieu* may constitute an important game fish. The most abundant populations of *M. d. dolomieu* occur where about 40% of the substrate consists of riffles flowing over clean gravel, boulder, or bedrock substrates with a maximum depth >1.2 m and gradients of 0.8–4.8 m/km, and where considerable water willow is present (Burton and Odum 1945, Trautman 1942, 1981).

Of particular interest is the small number of species found near the headwaters of streams in association with trout. Coker (1925) suggested that this situation may exist because of the relative high tolerance of brook trout to the typically lower pH of headwater streams compared to other species (e.g., Table 11) and the possible influencing interactions of temperature, current, and dissolved oxygen. Powers (1929) wrote that the commonly observed distribution of brook trout and rainbow trout (brook trout upstream, rainbow trout at lower elevations) might result from the presence or absence of dissolved organic substances. From their analyses of five streams in western Virginia, Burton and Odum (1945) concluded that temperature and stream gradient were the primary factors affecting longitudinal fish zonation.

On a broader scale, the geographic distribution of fish within the southern Appalachians has been extensively affected by anthropogenic disturbances. Presettlement fish distributions reflected drainage basin origins and extensive interbasin exchanges resulting from numerous headwater piracies (e.g., Ross 1969, 1971, Hocutt et al. 1978, Hocutt 1979; Chapter 2, this volume). Logging (e.g., Douglass and Seehorn 1974) and mining (e.g., Hill 1975) have been particularly detrimental to fish, especially brook trout. Introductions, whether purposeful or unintentional (minnow bucket introductions) have greatly modified fish faunas. Some of these factors are illustrated by the history of brook trout in the Great Smoky Mountains National Park (GSMNP).
TABLE 10 Typical Fish of High-Gradient Streams of the Southern Appalachian Mountains.

<table>
<thead>
<tr>
<th>Species</th>
<th>Common Name</th>
<th>Feeding Habits and References</th>
</tr>
</thead>
<tbody>
<tr>
<td>SALMONIDAE</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oncorhynchus mykiss</td>
<td>Rainbow trout</td>
<td>Insects and crustaceans; large individuals piscivorus; large individuals as much as 50% of diet may be terrestrial insects (Ricker 1934, Tebo and Hasler 1963, Carlander 1969)</td>
</tr>
<tr>
<td>Salmo trutta</td>
<td>Brown trout</td>
<td></td>
</tr>
<tr>
<td>Salvelinus fontinalis</td>
<td>Brook trout</td>
<td></td>
</tr>
<tr>
<td>COTTIDAE</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cottus baikdi</td>
<td>Mottled sculpin</td>
<td>Benthic aquatic insects (Ricker 1934, Daiber 1956)</td>
</tr>
<tr>
<td>CYPRINIDAE</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rhinichthys atratulus</td>
<td>Blacknose dace</td>
<td>Invertebrates; some plant material (Flemer &amp; Woolcott 1966, Minshall 1967, Tarter 1970)</td>
</tr>
<tr>
<td>R. cataractae</td>
<td>Longnose dace</td>
<td></td>
</tr>
<tr>
<td>Clinostomus funduloides</td>
<td>Rosyside dace</td>
<td></td>
</tr>
<tr>
<td>Phoxinus oresas</td>
<td>Mountain redbelly dace</td>
<td></td>
</tr>
<tr>
<td>Campostoma anomalum</td>
<td>Stoneroller</td>
<td>Primarily herbivorous; diatoms and filamentous algae (Flemer &amp; Woolcott 1966)</td>
</tr>
<tr>
<td>Notropis albeolus</td>
<td>White shiner</td>
<td></td>
</tr>
<tr>
<td>N. cornutus</td>
<td>common shiner</td>
<td>Omnivorous; terrestrial insects, algae, leaves (Breder &amp; Crawford 1922, Miller 1964)</td>
</tr>
<tr>
<td>N. rubellus</td>
<td>Rosyface shiner</td>
<td>Aquatic and terrestrial insects, (Pfeiffer 1955, Reed 1957, Miller 1964, Gruchy et al. 1973)</td>
</tr>
<tr>
<td>Species</td>
<td>Common Name</td>
<td>Diet</td>
</tr>
<tr>
<td>-------------------------------</td>
<td>---------------------</td>
<td>----------------------------------------------------------------------</td>
</tr>
<tr>
<td>N. photogenis</td>
<td>Silver shiner</td>
<td>Immature and adult aquatic insects; turbellarians (Gruchy et al. 1973)</td>
</tr>
<tr>
<td>N. spectrunculus</td>
<td>Mirror shiner</td>
<td>Nothing published</td>
</tr>
<tr>
<td>Nocomis leptocephalus</td>
<td>Bluehead chub</td>
<td>Omnivorous; selects plant food (Flemer &amp; Woolcott 1966)</td>
</tr>
<tr>
<td>N. micropogon</td>
<td>River chub</td>
<td>Benthic invertebrates; some plant material (Lachner 1950)</td>
</tr>
<tr>
<td>Semotilus atromaculatus</td>
<td>Creek chub</td>
<td>Benthic and terrestrial invertebrates; some plant material (Ricker 1934, Scott &amp; Crossman 1973)</td>
</tr>
</tbody>
</table>

**Percidae**

<table>
<thead>
<tr>
<th>Species</th>
<th>Common Name</th>
<th>Diet</th>
</tr>
</thead>
<tbody>
<tr>
<td>Etheostoma flabellare</td>
<td>Fantail darter</td>
<td>Aquatic insects (Forbes 1880, Turner 1921, Daiber 1956, Karr 1964)</td>
</tr>
<tr>
<td>E. longinanum</td>
<td>Longfin darter</td>
<td>Nothing published</td>
</tr>
<tr>
<td>E. Kanawhae</td>
<td>Kanawa darter</td>
<td>Nothing published</td>
</tr>
<tr>
<td>E. blennioides</td>
<td>Greenside darter</td>
<td>Aquatic insects (Forbes 1880, Turner 1921)</td>
</tr>
</tbody>
</table>

**Catostomidae**

<table>
<thead>
<tr>
<th>Species</th>
<th>Common Name</th>
<th>Diet</th>
</tr>
</thead>
<tbody>
<tr>
<td>Moxostoma rhothoeicum</td>
<td>Torrent sucker</td>
<td>Plant material (Flemer &amp; Woolcott 1966)</td>
</tr>
<tr>
<td>Catostomus commersoni</td>
<td>White sucker</td>
<td>Bottom feeder; algae, mollusks, chironomids (Flemer &amp; Woolcott 1966)</td>
</tr>
<tr>
<td>Hypentelium nigricans</td>
<td>Northern hog sucker</td>
<td>Scrapes and turns rocks: insects, crustaceans, diatoms (Flemer &amp; Woolcott 1966)</td>
</tr>
</tbody>
</table>

**Ictaluridae**

<table>
<thead>
<tr>
<th>Species</th>
<th>Common Name</th>
<th>Diet</th>
</tr>
</thead>
<tbody>
<tr>
<td>Noturus insignis</td>
<td>Margined madtom</td>
<td>Insects, fish? (Flemer &amp; Woolcott 1966)</td>
</tr>
</tbody>
</table>

Source: From Burton and Odum (1945), Neves and Pardue (1983), and Harshbarger (in preparation).
| $N. \text{cornutus}$ | common shiner | Omnivorous; terrestrial insects, algae, leaves (Breder & Crawford 1922, Miller 1964) |
| $N. \text{rubellus}$ | Rosyface shiner | Aquatic and terrestrial insects, (Pfeiffer 1955, Reed 1957, Miller 1964, Gruchy et al. 1973) |

TABLE 11 Distribution of Fish in Little Stony Creek, Virginia

<table>
<thead>
<tr>
<th></th>
<th>Headwaters</th>
<th>Downstream Gradient</th>
<th>Mouth</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elevation (m)</td>
<td>1120 1067 1021 981 939 922 917 905 838 754 667 603 556 515</td>
<td></td>
<td></td>
</tr>
<tr>
<td>pH</td>
<td>5.6 5.6 5.8 5.8 5.9 6.2 6.4 6.6 7.0 7.0 7.1 7.2 7.2 7.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temperature (°C)</td>
<td>15 15 16 16 17 18 18 18 19 19 20 20 21</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Brook trout</td>
<td>X X X X X X X X X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Blacknose dace</td>
<td>X X X X X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fantail darter</td>
<td>X X X X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rainbow trout</td>
<td>X X X X X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mottled sculpin</td>
<td>X X X X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stoneroller</td>
<td>X X X X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>White shiner</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Longnose dace</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>White sucker</td>
<td>X</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Source. From Burton and Odum (1945).
It is apparent that the range of brook trout in GSMNP is decreasing and has been decreasing for many years (Jones 1978, Kelley et al. 1980, Bevins et al. 1985). Brook trout are now restricted to small, high-elevation streams. This decline has been attributed to logging and associated habitat deterioration at lower elevations and to competition with introduced rainbow trout. Based on discussions with local fishermen, Powers (1929) found that brook trout had moved upstream prior to introduction of rainbows in 1919 and that the planting of rainbows was a response to this decline. Some of the fishermen attributed this decline to overfishing, but Powers noted that the decline was simultaneous with logging and that the distribution of brook trout was coincident with areas that had not been logged. However, with the regrowth of lower elevation forests, brook trout have not recolonized lower-elevation streams, and, in fact, the brook trout retreat is continuing (Jones 1978). The evidence for competitive displacement by rainbow trout is quite clear (Moore et al. 1983, Larson and Moore 1985). Populations of brook trout will probably persist in the high-elevation streams of GSMNP and throughout the southern Appalachians, though random extinctions of isolated populations in these marginal habitats should be expected (Larson and Moore 1985).

The fish of southern Appalachian streams are primarily insectivorous predators (Table 10). Trout, some of the dace, and some of the chubs are midwater and surface feeders, catching drifting aquatic invertebrates, terrestrial insects, and adult aquatic insects. Sculpins, darters, most chubs and minnows, and some dace feed predominantly on benthic invertebrates, searching on and

---

**TABLE 12** Percent Contribution by Fish Species to Annual Production in Three Sections of Guys Run, Virginia

<table>
<thead>
<tr>
<th>Species</th>
<th>Upper</th>
<th>Middle</th>
<th>Lower</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brook trout</td>
<td>60</td>
<td>61</td>
<td>14</td>
</tr>
<tr>
<td>Mottled sculpin</td>
<td>29</td>
<td>18</td>
<td>27</td>
</tr>
<tr>
<td>Blacknose dace</td>
<td>10</td>
<td>9</td>
<td>9</td>
</tr>
<tr>
<td>Torrent sucker</td>
<td>1</td>
<td>5</td>
<td>4</td>
</tr>
<tr>
<td>Bluehead chub</td>
<td>&lt;1</td>
<td>5</td>
<td>37</td>
</tr>
<tr>
<td>Fantail darter</td>
<td>&lt;1</td>
<td>&lt;1</td>
<td>&lt;1</td>
</tr>
<tr>
<td>Longnose dace</td>
<td>1</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>Rosyside dace</td>
<td>&lt;1</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Mountain redbelly dace</td>
<td>&lt;1</td>
<td>&lt;1</td>
<td>&lt;1</td>
</tr>
<tr>
<td>Rock bass</td>
<td>&lt;1</td>
<td>&lt;1</td>
<td>&lt;1</td>
</tr>
<tr>
<td>Smallmouth bass</td>
<td>&lt;1</td>
<td>&lt;1</td>
<td>&lt;1</td>
</tr>
<tr>
<td>Total fish production</td>
<td>2.84</td>
<td>3.16</td>
<td>3.96</td>
</tr>
<tr>
<td>(g/m² year⁻¹)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total fish biomass</td>
<td>2.14</td>
<td>2.56</td>
<td>4.74</td>
</tr>
<tr>
<td>(g/m²)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

among the rock and gravel streambed. Several species turn over small rocks in search of prey. Because of limited primarily production in these streams, plant feeders such as *Campostoma* occur only in somewhat larger streams with open canopy and lower gradient. Detritivorous fish are uncommon in high-gradient streams of the region. References to published feeding studies are given by Carlander (1969), Scott and Grossman (1973), and Lee et al. (1980).

Neves and Pardue (1983) estimated production of the fish community at three sites in Guys Run, Virginia (Table 12). Extrapolating from their study and comparing with other components of stream energetics, two conclusions are evident. First, fish predation pressure on stream invertebrates is considerable, but when probable sampling errors are taken into account, predation in not greater than estimated invertebrate production. Second, the fish community as a whole and brook trout in particular depend heavily on allochthonous energy sources. This connection is direct through feeding on terrestrial insects, and indirect through invertebrate dependence on allochthonous detritus. Thus, effects of forest logging and other disturbances on fish populations can be attributed to both lower water quality and modified food resources. Although data for fish production (Table 12), standing stock biomass (Table 13), and invertebrate production (Table 7 and 8) are from different streams, these data have important implications for fisheries biologists because they suggest the following: (1) Most small, high-gradient Appalachian streams, especially those draining areas dominated by crystalline rock, have relatively low levels of invertebrate production. (2) A considerable portion of this production is used by predaceous invertebrates. (3) In small, fishless, headwater streams secondary production of salamanders is similar to production of fish in larger downstream areas. (4) Secondary production of carnivorous vertebrates, especially those that rely on instream food resources, may be strongly influenced by availability of food resources.

**REPRESENTATIVE HIGH-GRADIENT STREAMS**

There are numerous small first- through fourth-order high-gradient streams in the southern Appalachians that can be considered representative or typical high-gradient streams. Many of these can be found on federal, state, and privately owned lands. In the southern Appalachians, we probably know less about the biotic structure and function of large, high-gradient rivers than smaller streams. This is attributable, at least in part, to the physical difficulty and expense involved in studying these larger rivers. Unfortunately, these rivers will probably come under increasing environmental pressure from municipal, industrial, and recreational interests to meet the growing population needs of the area.

Three rivers in the southern Appalachians were included in the original Wild and Scenic Rivers Act: the Chattooga River in Georgia, North Carolina, and South Carolina; the Obed River in Tennessee; and the headwaters of
<table>
<thead>
<tr>
<th>Parameter</th>
<th>Elevation (m)</th>
<th>Total fish biomass (g/m²)</th>
<th>Trout contribution (% of fish biomass)</th>
<th>Brook trout as (% of total trout numbers)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>&gt;1219</td>
<td>1.00</td>
<td>99.9</td>
<td>93.1</td>
</tr>
<tr>
<td></td>
<td>1067–1219</td>
<td>1.55</td>
<td>86.8</td>
<td>30.7</td>
</tr>
<tr>
<td></td>
<td>914–1067</td>
<td>1.74</td>
<td>63.5</td>
<td>29.7</td>
</tr>
<tr>
<td></td>
<td>762–914</td>
<td>2.10</td>
<td>26.6</td>
<td>30.7</td>
</tr>
<tr>
<td></td>
<td>610–762</td>
<td>2.10</td>
<td>33.0</td>
<td>30.7</td>
</tr>
<tr>
<td></td>
<td>457–610</td>
<td>2.15</td>
<td>36.3</td>
<td>7.8</td>
</tr>
<tr>
<td></td>
<td>&lt;457</td>
<td>1.66</td>
<td>25.7</td>
<td>5.8</td>
</tr>
</tbody>
</table>

Source: From Harshburger (in preparation).
TABLE 14 Some High-Gradient Creeks and Rivers in the Southern Appalachians That Were Included in the Nationwide Rivers Inventory Based on Outstanding Scenic, Recreational, Geologic, and Wildlife values

**Alabama**
Little Cahaba and Shoal Creek (Bibb and Shelby), Little River (Cherokee and DeKalb), Locust Fork of Black Warrior (Jefferson, Blount, Cullman, Marshall, and Etowah), and Mulberry Fork of Black Warrior (Blount and Cullman)

**Georgia**
Amicalola Creek (Dawson), Chattahoochee River (Hall, Habersham, and White), Chattooga River* (Rabun and also South Carolina), Chestatee River (Lumpkin), Conasauga River (Gordon, Whitfield, and Murray), Coosawatee River (Gilmer), Etowah (Bartow and Floyd)

**Kentucky**
South Fork and Little South Fork of Cumberland (McCreary and Wayne), Martins Fork (Harlan and Bell), Rock Creek (McCreary), Tygarts Creek (Carter)

**Maryland**
North Branch of Potomac, Savage*, and Yougigoheeny Rivers* (Garrett)

**North Carolina**
Big Laurel Creek (Madison), Cane River (Madison), Davidson River (Transylvania), Green River (Polk), Linville River (Burke and Avery), Mitchell River (Surry and Alleghany), Nanahala River (Swain and Macon), Oconaluftee (Swain), Tellico (Cherokee), Tuckasegee (Swain and Jackson), Watauga (Watauga and Avery), and Yadkin (Davidson)

**South Carolina**
Chauga River (Oconee)

**Tennessee**
Abrams and Anthony Creeks (Blount), Clear Creek (Morgan, Fentress, and Cumberland), Conasauga River (Bradley and Polk), East Fork of Obed (Fentress and Overton), French Broad (Knox and Sevier), Hiwassee and Ocoee Rivers (Polk), Piney Creek (Rhea), South Fork of Cumberland (Scott), and Tellico (Monroe)

**Virginia**
Bullpasture and Cowpasture Rivers (Allegheny, Bath, and Highland), Dan River (headwaters, Patrick), South Fork of Holston River (Washington), Jackson River (Allegheny, Bath, and Highland), Back Creek (Bath and Highland), Little River (Pulaski, Montgomery, and Floyd), Maury River (Rockbridge), New River* (Grayson, Carroll, and Pulaski), Cedar Creek (Shenandoah and Frederick), Passage Creek (Shenandoah), South Fork of Shenandoah River (Warren and Page), Stony Creek* (Giles)

**West Virginia**
Big Sandy Creek (Preston), Birch River (Nicholas and Braxton), Blackwater River (Tucker), Bluestone River (Mercer and Summers), Buckhannon River (Barbour, Upshur, and Randolph), Cacapon (Morgan, Hampshire, and Hardy), Cheat...
 RESOURCE USE AND MANAGEMENT EFFECTS

TABLE 14 (Continued)

River including Dry Fork, Glady Fork, Shavers Fork (Tucker and Randolph), Elk River (Braxton, Webster, and Randolph), Gauley River including Cherry and Cranberry rivers (Greenbrier, Nicholas, Webster, Pocahontas, and Randolph), Greenbrier River (Pocahontas), Meadow River (Nicholas, Fayette, and Greenbrier), Middle Fork River (Barbour, Upshur, and Randolph), North and South Branches of Potomac River (Grant, Pendleton, Hardy, and Highland), Tugart Valley River (Barbour, Taylor, and Marion).

Note. Streams are listed by state and counties in which they are located are in parentheses. The list is not intended to be complete. Those marked with an asterisk were added by the authors. For additional streams and information about each consult National Park Service (1981).

the New River in North Carolina. In addition to these streams, numerous other examples of large high-gradient creeks and rivers can be found in the first Nationwide Rivers Inventory of the National Park Service (1981).

The purpose of the National Park Service’s survey was to provide congress, federal, state, and local government agencies, and the private sector with comprehensive consistent data on the nation’s free-flowing streams, which could be used to: (1) provide baseline data on the condition and extent of significant free-flowing river resources so that they can be monitored over time; (2) provide informed decisions on river use for recreation, water supply, irrigation, hydroelectric power, flood control, and conservation of scenic and wild rivers; (3) assist and encourage state, local, and private efforts to conserve rivers; and (4) permit comparisons with the National Scenic and Wild River system and identify other rivers that would complete the system. The following criteria were applied to streams selected in the First Nationwide Rivers Inventory: Rivers must appear 25 miles or longer on 1:500 000 scale maps; dammed or channelized rivers were not considered; excessive cultural development such as cities of >10 000 in population, power plants, and active strip mines within 400 m of the bank excluded streams from consideration; the river must have sustained flow; and, the river had to pass field and helicopter video analyses. The list of the nation’s rivers did not include rivers presently in, or in consideration for, the National Wild and Scenic River system. Some examples of streams included in the first survey are listed in Table 14.

RESOURCES USE AND MANAGEMENT EFFECTS

A survey of 231 individuals engaged in natural resource management who represented private industry and local, state, and federal governments in a 22-county area of western North Carolina indicate that the most important management priority is the maintenance of high-quality streams (SARRMC 1977). This survey concluded that both the general public and municipal leaders view severe stream degradation as their greatest resource problem.
Identification of the sources, composition, and quantities of wastes and runoff contributing to stream degradation was viewed as the most important research target (SARRMC 1977). Municipalities, manufacturing, recreational, and energy (hydroelectric) interests, combined with forest management (logging) place increasing demands on southern Appalachian streams where heavy rainfall, combined with a dense forest cover, gives rise to many clean streams. Since the late 1970s, there has also been growing public awareness of the potential problems associated with acidic precipitation. Acidic precipitation may present serious problems in the immediate future for streams draining the crystalline regions of the Appalachians. Coal mining also represents an ongoing problem for many Appalachian streams.

Sewage and industrial effluents can produce pronounced effects on water quality and on both microbial and macroinvertebrate community structure within small Appalachian streams. Kondratieff and Simmons (1982) and Kondratieff et al. (1984) reported that the macroinvertebrate community of Cedar Run, Virginia, consists of a diverse assemblage of all functional groups in upstream reference sections compared to a community dominated by collector-gatherers below areas of waste outfall. Farther downstream, collector-filterers constituted the majority of the macroinvertebrate community. Macroinvertebrate scraper biomass was much lower at heavily polluted sites compared to reference stations located upstream and several kilometers downstream of outfalls. The effluents seriously disrupted the integrity of the macroinvertebrate community and microbial community response paralleled that of the macroinvertebrate community. At reference stations in Cedar Run, microbial assemblages were dominated by autotrophs, primarily diatoms, whereas heterotrophic microbiota predominated below waste outfalls (Kondratieff et al. 1984). All of the particulate organic carbon (POC) added by the sewage effluent was removed from the water column within 3 km downstream. Kondratieff and Simmons (1982) suggested that biological uptake by filter-feeding macroinvertebrates and microbial decomposition were responsible for the majority of POC removal. Although organic effluents produce significant alterations in stream biota, the tolerant species may assume an important role in processing these excessive inputs and enhance the self-purification capacity of the stream. Reports of various state agencies represent valuable resources for additional documentation of stream degradation by municipal and industrial waste, for example, The Georgia Water Quality Control Board (GWCB 1970) and the Benthic Macroinvertebrate Ambient Network (BMAN 1985) in North Carolina.

Watershed disturbances such as clear-cutting may produce a multitude of both short- and long-term changes in stream ecosystems. Sedimentation resulting from logging and associated practices such as road building may produce an immediate impact on stream biota (Tebo 1955, Gurtz and Wallace 1984). Clear-cutting increases stream temperatures (Swift 1983, Swift and Messer 1971). Clear-cutting also shifts the relative abundance of allochthonous to autochthonous inputs, which may shift the energy base of the stream (Webster et al. 1983) and be reflected in the invertebrate community (Woodall
and Wallace 1972, Webster and Patten 1979, Haefner and Wallace 1981b, Gurtz and Wallace 1984, Wallace and Gurtz 1986). There may also be long-term changes in benthic organic matter storage, especially woody debris (Golloday et al. 1989). Although wood decomposes slowly (Triska and Cromack 1981, Golloday and Webster 1988), there is little input of woody debris other than slash added to the stream during logging, until the forest regenerates. Likens and Bilby (1982) and Hedin et al. (1988) suggested that recovery of streams may lag behind, or be out of phase with that of the terrestrial forest, since large stable debris dams will be reestablished only after mature trees die and fall into the stream channel. Thus, while total allochthonous inputs may be restored to the stream channel within 6–10 years of forest regrowth, the absence of large woody debris dams may influence retention characteristics of the stream for many decades (Webster et al. 1990).

The impact of forest fire on stream biota in the Appalachians is not well known. Most studies of fire have been confined to western North America (Wright and Bailey 1982, Minshall et al. 1989). Some of the immediate effects of severe fire from these western studies appear to resemble those of clear-cutting. These include elevated stream temperatures, increased sediment loads, and, increased nutrients and primary productivity, which may stimulate secondary production of some aquatic insects. However, the increased sediment loads may destroy spawning sites for fish and increased stream temperatures following destruction of the canopy cover may lead to higher incidence of fish disease (Wright and Bailey 1982). Long-term effects may parallel those outlined for clear-cutting (Minshall et al. 1989).

Acid mine drainage is an important source of pollution in coal mining areas of the Appalachians. Groundwater and water percolating through spoil banks may contain sulfuric acid as well as various metallic salts. Iron sulfides, especially pyrite (Fe$_2$S$_2$), react with water in the presence of oxygen to form sulfuric acid. In addition, substrates in stream channels draining mined areas are often coated with reddish-yellow deposits of ferric hydroxide. Typically, streams having acid mine drainage problems have high conductivities, higher iron and sulfate concentrations, and lower pH and alkalinitis than streams draining unmined watersheds in the region (Herricks and Cairns 1974).

Between the years 1930 and 1971, some 2017 km$^2$ of the southern Appalachians were surface mined. About 32–48% of this area was not reclaimed, and abandoned mines represent an ongoing problem (Samuel et al. 1978). Streams draining abandoned mines have reduced invertebrate and fish populations for up to two decades following cessation of mining operations. In some cases, Odonata, Ephemeroptera, and Plecoptera have been completely eliminated, while the Trichoptera, Megaloptera, and Diptera species have been severely affected (Roback and Richardson 1969). Some streams such as Shavers Fork, West Virginia, show increasing degradation since the early 1960s that is associated with increased mining operations. Acid “slugs,” released from mined areas during high spring runoff, appear to be the main factor contributing to degradation of Shavers Fork (Samuel et al. 1978). Tarter (1976) noted that coal mining and industrialization, especially chemical plants,
have polluted many streams in some regions of West Virginia to the extent that only the most tolerant species of benthic organisms can inhabit them.

The impoundment of many Appalachian streams for hydroelectric and recreational purposes has been a controversial topic since the early 1900s. Obviously, community structure is altered from lotic to lentic conditions within the area of stream inundated. However, in the last two decades it has become increasingly evident that impoundments produce major modifications on the biota below dams. Ward and Stanford (1983) and Ward (1984) addressed some of the changes induced by stream regulation, including altered thermal regimes, which may produce winter-warm or summer-cool conditions below deep release dams creating thermal regimes that are intolerable by many species. Flow regimes may also be very different from that of unregulated streams and eliminate certain species. Dams may alter the ratio of CPOM/FPOM supplied to downstream areas as well as altering the quality of FPOM. Particles suspended in the water column of lake outlets have high nutritive value (Kondratieff and Simmons 1984, Voshell and Parker 1985). Provided species can tolerate the altered thermal regimes, the enriched seston may result in abundant filter-feeder production (Voshell 1985, and Table 7).

The gypsy moth, *Lymantria dispar* (L.), feeds on the foliage of over 600 deciduous and coniferous plants. This forest pest has the potential ability to impact small, high-gradient streams of the Southeast by several mechanisms. Heavy insect defoliation by the fall cankerworm, *Alsophila pometaria* (Harris), has been shown to increase nitrate (NO$_3$-N) export from southern Appalachian watersheds, which influences watershed nutrient budgets (Swank et al. 1981). Severe defoliation also influences leaf production, frass, and nutrient inputs to the forest floor and stream (Swank et al. 1981), which may increase insolation of the stream and alter the timing, quantity, and quality of stream energy resources. Furthermore, aerial spraying with pesticides to control forest pests may induce catastrophic drift of stream invertebrates (Wallace and Hynes 1975) and, in instances where persistent chlorinated hydrocarbon pesticides were used to control forest pests, benthic populations may be reduced for several years (Ide 1967). Recently, Swift and Cummins (1991) reported that leaf litter from trees previously sprayed with the insecticide Dimilin, which is widely used for gypsy moth control, increased mortality of aquatic shredders feeding upon leaves from sprayed compared to unsprayed plots.

There are currently few data indicating that acidic precipitation has produced significant changes in the biota of southern Appalachian streams. This reflects the absence of long-term data bases and does not imply that this is an area for little concern. Trend analysis of precipitation chemistry does indicate the need for concern (Schertz and Hirsch 1985). Lynch and Dise (1985) suggested that all basins in the Shenandoah National Park (SNP) in Virginia show some signs of acidification by atmospheric deposition. In the SNP, streams draining resistant siliceous bedrocks are viewed as extremely sensitive (alkalinity <20 μeq/L) and those draining granitic rock as having a high sensitivity to acid deposition (alkalinities of 20–100 μeq/L) (Lynch and Dise 1985). However, Messer et al. (1986) examined 54 randomly selected
streams in the southern Blue Ridge during the spring and found that despite generally circumneutral pH values, the majority of the streams possessed relatively low acid neutralizing capacity (ANC). Messer et al. found that 6.3% of the combined stream length possessed ANC of <20 μeq/L, while 74.4% were estimated to be <200 μeq/L.

In other regions subject to acidification, episodic runoff, especially that associated with snowmelt, may increase the solubility of aluminum in stream water (Hall et al. 1985). The downstream drift rate of some species of invertebrates, especially mayflies, chironomids, and blackflies, increases with either the addition of strong acids (Hall et al. 1980, 1982) or aluminum chloride (Hall et al. 1985). These results are consistent with those from Scandinavia that report altered macroinvertebrate community structure associated with acidified streams (Drablos and Tollan 1980). Community structure of algae in streams of the GSMNP was found to differ among high and low pH sites. The highly acidic sites had high cell biovolume, chlorophyll a density, and areal primary productivity compared to sites with higher pH (Mulholland et al. 1986). In contrast, decomposing leaf litter at low-pH sites in the GSMNP had lower microbial production and respiration rates compared to high-pH streams (Palumbo et al. 1987).

In the northeastern United States, Canada, and Scandinavia, where soils and water have little buffering capacity, all trophic levels of aquatic ecosystems (decomposers, primary producers, primary and secondary consumers) appear to be affected by acidification (Haines 1981, Drablos and Tollan 1980). In the southern Appalachians, streams draining high-elevation watersheds with shallow soils underlain by siliceous and granitic bedrock are thought to represent areas most sensitive to acidic precipitation (Record et al. 1982). For example, Silsbee and Larson (1982) found that bacterial densities, pH, alkalinity, turbidity, as well as concentrations of Na, K, and Si decrease with increasing stream elevations in the GSMNP. Bedrock geology had a strong influence on pH, alkalinity, conductivity, hardness, and concentrations of several elements.

RECOMMENDATIONS FOR FUTURE RESEARCH AND MANAGEMENT

Since the early 1900s, there have been numerous conflicts between industries, logging and mining interests, municipalities, private citizens, and the federal government over land and stream use in the southern Appalachians. Mastran and Lowerre (1983) provide an excellent and entertaining historical perspective of these conflicts that have shaped the development of the Appalachian landscape. Unfortunately, many of the conflicts remain unresolved. Many inhabitants of the region voice open opposition to the creation of more wilderness areas for several reasons: (1) the ban on logging in wilderness areas; (2) loss of county tax revenues; (3) exclusion of motorized vehicles; (4) the “invasion” of wilderness areas by “outsiders”; (5) the threat to private own-
ership within and adjacent to wilderness areas; and, (6) rights of individuals versus rights of the federal government (Mastran and Lowerre 1983). While these issues are not easily resolved, there are others for which solutions do exist.

Clearcut logging, road, residential, and industrial construction, and agricultural practices have and continue to be conducted with little regard for environmental influences on streams that drain Appalachian watersheds. In some areas, coal mining and industrial and municipal pollution represent ongoing problems for Appalachian streams. These operations contribute to both point and nonpoint sources of stream pollution.

In most cases adequate knowledge exists to sharply curtail such stream degradation. The main problems are the absence of adequate laws or the enforcement of existing laws, and the absence of adequate transfer of technology from researchers to those engaged in forest management, agriculture, and industrial, municipal, urban, and rural residential development. Responsibility resides with all aspects of society, including government, researchers, developers, manufacturers, business, and private citizens. For example, early work in the Appalachian region showed that roads contribute to sediment inputs into streams. Proper design of forest access roads can reduce >90% of the sediment input into streams according to Swift (1988), who also noted, “Guidelines for forest road design are available which minimize the impact of construction and use on water quality. The task is to apply these guidelines.” Implementation of proper design of spoil banks and adequate reclamation of surface mined sites could also greatly reduce the impact of acid mine drainage on streams in coal mining regions (see Samuel et al. 1978).

Unfortunately, as long as government officials, corporation and business interests, and private citizens continue to have strong vested economic considerations in practices that may directly or indirectly contribute to stream degradation, there will continue to be environmental degradation of waterways.

For watershed disturbances such as clear-cutting or other major disturbances where both the physical environment and energy inputs to the stream are altered, any return of the biota to some resemblance of a predisturbance configuration may require long-term (>50 years) studies (Webster and Swank 1985b, Wallace et al. 1986). Extensive long-term data and more knowledge on the exact mechanisms and consequences for ecosystem level processes are required to adequately assess the potential influence of acidic precipitation on stream biota. Unfortunately, we lack sufficient long-term data bases to document the potential subtle effects of acidification, or other pollutants, on stream biota in most streams. It has been almost 30 years since Hynes (1960, p. 174) clearly stated the necessity for long-term studies as follows: “In the past, when damage has been caused or suspected, it has usually been impossible to estimate what was the previous biological condition of the water, except by inference. If records existed the fact of increased or decreased damage could easily and quickly be estimated.” The need for such long-term studies appears to be as great today as it was when Hynes stated the problem.
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