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Functional structure and production of the benthic community in a Piedmont river: 1956–1957 and 1991–1992

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Abstract

Taxonomic composition and functional group abundance, biomass, and annual production were measured in 1991–1992 for the macroinvertebrate community in a Piedmont river. Abundances and biomass values were influenced by standing crops of *Podostemum ceratophyllum,* a hydrophyte which covered bedrock substratum. Collector-filterers, collector-gatherers, and scrapers dominated functional-group abundance; scrapers and collector-filterers dominated biomass. Benthic production was 181.9 g ash-free dry mass m^{-2} yr^{-1}; 57% was attributable to collector-filterer hydropsychid caddisflies and 13% to a scraper snail. Results were compared to a previous study conducted at the same site in 1956–1957. Physical parameters of temperature and discharge regimes, *P. ceratophyllum* standing crops, and riparian vegetation were similar between studies, but marked changes in land use had occurred within the catchment. Benthic community structure was dominated by small, multivoltine collector-gatherers and microfilterers in 1956–1957; in 1991–1992 dominant taxa consisted of larger, longer lived macrofilterers and scrapers. Changes in community structure and indices of biotic integrity indicate stream condition improved in 1991–1992 relative to 1956–1957; changing land-use practices are implicated as the key factor for improvement.

The monitoring of stream and river resources has made a fundamental and philosophical shift in recent years. Traditionally, monitoring procedures called for direct measurement of water quality parameters (e.g. pH, temperature, dissolved oxygen, and chemical constituents) and comparison of results to water quality standards (Karr 1991). This approach alone is often inadequate as it does not account for cumulative effects of multiple contaminants which singularly fall within standard limits. Development of toxicity testing procedures overcame this shortfall by providing a more holistic approach for assessing impacts of contaminants on the biota, and multispecies or microcosm-mesocosm procedures further improved testing by indicating how contaminants affected biotic interactions (Karr 1993). However, these approaches still could not adequately monitor stream resources, as stream systems are also impacted by mechanisms other than water quality contamination, including alterations of food resource availability (trophic base), modification of habitat quality and availability, changes in flow regime, and influences on biotic interactions through species introduction or extirpation (Karr 1991, 1993).

A third approach has emerged based on biological monitoring of the ambient community to assess stream biotic integrity, or the ability of lotic systems to "support and maintain a balanced, integrated, adaptive community of organisms having a species composition, diversity, and functional organization comparable to that of natural habitat of the region" (Karr and Dudley 1981, p. 56). Biotic integrity is assessed by comparing taxonomic and functional structure of the stream community to that of unimpacted reference sites or sets of expected criteria. Ambient biotic monitoring has advantages over other monitoring approaches by providing a direct evaluation of stream resource condition, by integrating cumulative impacts from a wide range of potential perturbations, and by relating easily to the general public (Karr 1993).

Specific techniques, protocols, and indices used to assess biotic integrity have been developed that focus on the benthic macroinvertebrate community (Lenat 1988; Plafkin et al. 1989; Lenat 1993). These procedures often use taxonomic tolerance values to indicate susceptibility of individual taxa to environmental perturbation. Assessments of biotic integrity are generally used to address existing stream conditions; however, applying indices to comparative historical and contemporary data can provide insight into how benthic communities have responded to long-term anthropogenic changes in a lotic system or its catchment.

Comparative studies of benthic community structure after extended time intervals have shown different responses of aquatic biota to long-term anthropogenic impacts. Ward (1975) found community structure in North St. Vrain Creek (Colorado) remained essentially unchanged relative to a study conducted 29 yr earlier, despite a substantial increase in riparian vegetation cover. Haefner and Wallace (1981) repeated a study conducted

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in a disturbed southern Appalachian stream and reported major differences in benthic composition and functional structure following 10 yr of old-field succession. Heckman (1981) resampled orchard drainage ditches in northern Germany after 25 yr of intensive pesticide usage and found substantial reduction in taxonomic richness and shifts in benthic composition.

The Piedmont geophysical province of the southeastern U.S. has received varying degrees of anthropogenic influence since the 18th century. Historically a region of cotton and corn agriculture, intensive farming practices have impacted rivers through increased suspended sediment loads, elevated nutrient inputs, and pesticide runoff (Crawford and Lenat 1989). Studies that compare benthic community structure in streams of agricultural catchments to less impacted systems indicate lower taxonomic richness in agricultural streams, especially for intolerant fauna such as Ephemeroptera, Plecoptera, and Trichoptera (Lenat 1984; Crawford and Lenat 1989). Tolerant taxa, such as many Chironomidae and Simuliidae dipterans, have been shown to increase in richness and abundance in streams receiving agricultural pesticides (Heckman 1981). Increased nutrient loads can alter the stream trophic base (Lenat 1984; Crawford and Lenat 1989), and pesticide inputs may impact producer-herbivore or herbivore-carnivore interactions (Heckman 1981). Secondary production of stream benthos can also be affected by stress resulting from pesticides (Lugthart and Wallace 1992) or alterations of the trophic base (Wallace and Gurtz 1986).

Since the early 20th century, land use in the region has steadily moved away from intensive cotton and corn rowcropping, and reduction of agriculture has reduced inputs of sediments, nutrients, and pesticides to stream systems (Mulholland and Lenat 1992). Investigations which describe functional structure and secondary production of benthic communities are uncommon for Piedmont rivers (Mulholland and Lenat 1992), and we are aware of no studies that directly address how benthic community structure and stream biotic integrity respond to long-term reduction of agricultural land use.

The objective of this paper is to characterize taxonomic composition and functional structure (abundance, biomass and secondary production) of the benthic macroinvertebrate community in a Georgia Piedmont river. We compare our results to those of Nelson (1957) and Nelson and Scott (1962), who described benthic composition and structure at the same location 35 yr before our study to assess how changing land-use practices in the catchment over time may have influenced macroinvertebrate community structure and biotic integrity in this Piedmont river ecosystem.

Study area

The study was conducted in a 100-m reach of extensive bedrock outcrops (shoals) in the Middle Oconee River, a sixth-order tributary of the Altamaha River system in Athens-Clarke County, Georgia. At the study site, the river is ~60 m wide with a drainage basin of 1,030 km^2. Streambed slope is generally moderate (~1.4-m fall per 1-km distance); however, within the shoals slope is steep (~1.0-m fall per 10-m distance). Substratum is irregular bedrock and large boulders; areas below the shoals are primarily coarse, shifting sands. At baseflow conditions, water depths vary from several centimeters to >50 cm.

Similar to other rivers of the Piedmont region (Mulholland and Lenat 1992), shoaled reaches of the Middle Oconee support dense stands of *Podostemum ceratophyllum* (Michaux), a rootless hydrophyte with holdfast structures that enable it to tolerate relatively high current velocities by attachment directly to bedrock and boulder substrata. Plant stems reach a length of 10–20 cm before dividing into reduced leaves which form a thick overstory above the bedrock. Beneath this overstory, a thin layer (~1 cm thick) of mixed sands covers the bedrock substratum.

In 1956–1957, a 13-month study characterized the benthic macroinvertebrate community associated with this bedrock outcrop reach of the river (Nelson 1957; Nelson and Scott 1962). The study identified macroinvertebrate taxa, quantified abundance and biomass at various trophic levels, and is the earliest work cited by Benke (1993) that estimated total secondary production for the macroinvertebrate community. Descriptions and photographs of the study site provided by Nelson (1957) and Nelson and Scott (1962) indicate that shoals and adjacent wooded riparian areas remain relatively unchanged since 1956–1957 (Fig. 1).

Although riparian areas changed little, land-use practices in the Middle Oconee basin have changed greatly, both before and after the original study. In the Piedmont region, widespread forest clearing coupled with cotton and corn agriculture began in the 18th century and peaked in the late 19th and early 20th centuries (Mulholland and Lenat 1992). In the 20th century, often in response to soil depletion, Piedmont farmland returned to forested areas through abandonment or conversion to pine plantations (Mulholland and Lenat 1992). In the Georgia counties of Barrow, Clarke, and Jackson (which include most of the Middle Oconee catchment), over 800 km^2 (64–85% of total area) were in cropland, primarily cotton and corn, at the beginning of the 20th century (Fig. 2). Reflective of the entire Piedmont region, cropland in the Middle Oconee basin steadily diminished in the 20th century; by the mid-1950s ~40% of basin area was in farmland and 10% in cotton and corn. When our study was conducted in 1991–1992, <20% of the basin was cropland, none of which was in cotton and corn (Fig. 2).

Long-term data sets of daily discharge and water temperature are available for the study site. Since 1937, the U.S. Geological Survey (USGS) has operated a water-stage recorder on the river. Calculated daily discharge readings from this gauge, which is ~500 m downstream of the study site, are published annually by the USGS. Drinking-water intakes for the city of Athens are also located immediately downstream of the study area, and records of daily water temperatures are kept. Measures of water chemistry and total suspended solids have been

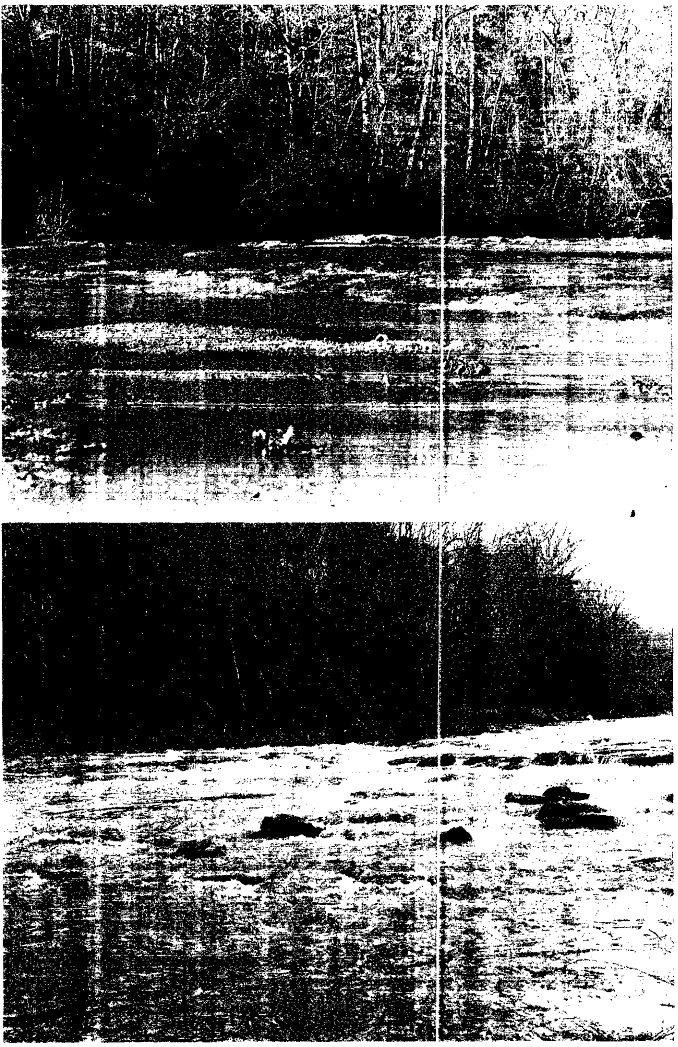

Fig. 1. Bedrock-outcrop habitat of the Middle Oconee River shoals in 1956–1957 (above) and in 1991–1992 (below). Mean daily discharge was 5.1 $m^3 s^{-1}$ in 1956–1957 and 9.7 $m^3 s^{-1}$ in 1991–1992. Note thickly wooded riparian areas were present in both 1956–1957 and 1991–1992. (Upper photograph from Nelson 1957.)

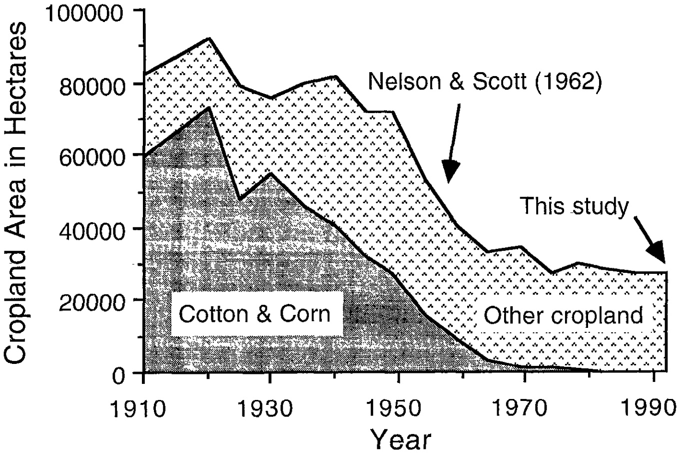

Fig. 2. Agricultural land use in the Middle Oconee River basin from 1910 to 1990. Data are from agricultural censuses of Barrow, Clarke, and Jackson Counties (U.S. Dep. Commerce 1910–1988), which make up most of the catchment area for the river. Total cropland and cropland planted in cotton or corn are shown; the 1956–1957 study period (Nelson and Scott 1962) and 1991–1992 study period (this study) are indicated by arrows.

taken sporadically at the site over the past 35 yr with a variety of collection and analysis techniques; however, these data were not included because of their limited and variable nature.

Methods

From September 1991 to August 1992 benthic samples were collected monthly from the Middle Oconee River study area. Sampling procedures were designed to closely match those used in 1956–1957 (Nelson 1957; Nelson and Scott 1962). On each sampling date five replicate samples were taken with a modified T-sampler (Merritt and Cummins 1984) having a sampling area of 103 cm^2 and fitted with a 230-μm-mesh catch net; Nelson (1957) used a 100-cm^2 Surber frame fitted with ~0.2-mm catch net in 1956–1957. Collections during both studies were confined to midstream areas to avoid bedrock which might dry out during low-flow conditions. Samplers were pressed against the bedrock so that the *P. ceratophyllum* mat formed an effective seal between bedrock and sampler. Bedrock was scraped clean of *P. ceratophyllum* and associated macroinvertebrates with a putty knife. In 1991–1992, collected material was preserved in the field in 5–10% Formalin containing Phloxine-B dye to aid in sample processing.

In conjunction with 1991–1992 sampling, measurements were made of current velocities above and below the *P. ceratophyllum* overstory. A velocity stick was used for current above the overstory (Wilm and Storey 1944); differences in water head height between sharp and blunt sides of the stick were converted to velocity estimates. For estimates below the hydrophyte overstory, differences in head readings between a straight and Pitot tube were used.

Samples were washed through 1-mm and 250-μm nested sieves to remove organisms not attached to *P. ceratophyllum*. Plant material was examined under 15× magnification to recover attached organisms, and invertebrates subsequently collected were added to sieved material. Material retained on the 1-mm sieve was sorted at 15× magnification and all macroinvertebrates were removed. Material retained on the 250-μm sieve was subsampled with a sample splitter (Waters 1969) before removing organisms under 30× magnification.

P. ceratophyllum from each sample was dried at 60°C for 5–7 d, weighed, ashed at 550°C for 12 h, then reweighed to determine ash-free dry mass (AFDM). Monthly standing crops of *P. ceratophyllum* are expressed as g

AFDM m^{-2} ±1 SE. Net annual apparent productivity (Nelson and Scott 1962) was estimated by the addition of increases in standing crops between successive sampling dates. This results in a crude estimate of annual production, but provides a comparative value between studies.

Insect and molluscan identifications were generally made to genus or species, exceptions being Sphaeriidae (Bivalvia), and the Chironomidae (Diptera) which were identified as Tanypodinae and non-Tanypodinae. Nematoda, Turbellaria, Oligochaeta, Cladocera, Copepoda, and Hydracarina were identified no further than these taxonomic categories. Macroinvertebrates were assigned to one of five functional feeding groups based on morphobehavioral mechanisms of food acquisition (Cummins 1973). Functional feeding groups designations (from Merritt and Cummins 1984) are as follows: scrapers—feed on aufwuchs from various substratum surfaces (e.g. rock, woody debris, and vascular hydrophytes); shredders—feed on live or detrital plant tissue (coarse particulate organic material); collector-gatherers—feed on deposited fine particulate organic material; collector-filterers—feed on entrained materials (detrital, microbial, algal, or animal) in the water column; predators—feed on other macroinvertebrate fauna by engulfing prey.

Individual functional group assignments were made in accordance with Merritt and Cummins (1984) and Lugthart and Wallace (1992). Following identification, organisms were measured (total body length) to the nearest millimeter and individual biomass calculated from predetermined length-weight regression equations (bivalve shells were removed before determining AFDM for regression equations). Abundances and biomass values are expressed as individuals m^{-2} or mg AFDM m^{-2} ±1 SD.

To test for differences between abundances and between biomass values, we used Sheffé's multiple contrast procedure (Zar 1984). Means of abundances and biomass values were positively correlated to standard deviations; thus data were $\log_{10}(X + 1)$ transformed before statistical analyses to eliminate heteroscedasticity.

Annual production estimates for most taxa were calculated with the size-frequency method (Hamilton 1969) corrected for cohort production interval (CPI, Benke 1979). CPIs were estimated by examining size-frequency distribution of taxonomic abundances across sampling dates. *Hydropsyche* spp. and *Cheumatopsyche* spp. (Trichoptera: Hydropsychidae) were assigned CPIs of 122 d, based on life-history patterns from a nearby Georgia Piedmont stream (Freeman and Wallace 1984). Non-Tanypodinae chironomid production was estimated with the community-level method (Huryn 1990), which incorporates annual thermal variation into calculations of daily growth rates. We assumed a production to mean annual biomass ($P:B$) ratio of 5 for Nematoda, Oligochaeta, Turbellaria, and Hydracarina. For Cladocera and Copepoda, we assumed $P:B$ ratios of 10 and 18 (Lugthart and Wallace 1992).

Because a 35-yr interval separated this study from the 1956–1957 study, we used a conservative taxonomic approach to avoid interpreting changes in systematics as shifts in the taxonomic composition of the macroinvertebrate community. Taxa collected in 1991–1992 that had been considered a single taxon in 1956–1957 (e.g. *Ephemerella* spp. and *Serratella* spp.) were grouped as one taxon for interstudy comparisons. If taxonomic keys available in 1956–1957 did not clearly separate taxa (e.g. *Cheumatopsyche etrona* from *Hydropsyche* spp.), interstudy comparisons were made at the familial level. Furthermore, trophic designations assigned by Nelson and Scott (1962) were not used for comparisons of functional composition. Rather, macroinvertebrates collected in 1956–1957 were reassigned to functional groups in accordance with Merritt and Cummins (1984) and Lugthart and Wallace (1992).

Four indices were used to compare changes in biotic integrity between the two studies. These included total taxa richness, percent contribution of the dominant taxon, number of Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa (*see* Crawford and Lenat 1989), and the North Carolina Biotic Index (NCBI), which is specific to the southeastern U.S. (Lenat 1993). Taxa richness and EPT are tallies of distinct taxa which generally decrease as stream systems are stressed (Crawford and Lenat 1989; Plafkin et al. 1989). Percent contribution of the dominant taxon is based on macroinvertebrate abundance and is a measure of evenness of the benthic community; a community dominated by one or few taxa is often indicative of environmental stress (Heckman 1981; Plafkin et al. 1989). Non-Tanypodinae Chironomidae were excluded as a dominant taxon when calculating this index because of potential bias resulting from our limited classification of this group.

The NCBI uses a list of assigned tolerance values (TVs) ranging from 0 (lowest tolerance) to 10 (highest tolerance) for specific benthic fauna, based on an extensive data set of macroinvertebrate stream samples from mountain, Piedmont, and coastal regions of North Carolina (Lenat 1993). The index is calculated as the sum of each taxon's abundance multiplied by its TV, divided by total abundance, and weighted for seasonal differences (Lenat 1993). TVs are generally assigned to species; to apply the NCBI to genus and familial-level classifications of comparative Middle Oconee River benthic data, we used TVs from species likely to occur at the study area. When more than one species from a given genus was known to occur at the study site (i.e. *Hydropsyche* spp.), we used a mean TV from all possible species, and TVs for specific taxa were kept consistent between studies. Because of these changes we refer to our use of this index as a modified NCBI and report TVs assigned to various taxa in Table 1. Individual NCBIs were calculated monthly from 1956–1957 and 1991–1992 data sets and mean NCBIs from each study period were used for comparison.

Results

Current velocities above the *P. ceratophyllum* overstory ranged from 0.3 to 1.7 m s^{-1} (mean, 0.9 m s^{-1}) during sampling. Velocities were significantly reduced ($P < 0.001$,

Table 1. Tolerance values (TVs) of taxa collected from bedrock-outcrop habitat by Nelson (1957) in 1956–1957 and during this study in 1991–1992. Key to superscripts: 1—includes *Baetis* spp. and *Heterocloeon* sp.; 2—includes *Ephemerella berneri* (Allen and Edmunds), *Ephemerella dorthea* (Needham), *Ephemerella rossi* (Allen & Edmunds), *Serratella deficiens* (Morgan), and *Serratella serratoides* (McDunnough); 3—includes *Stenonema modestum* (Banks); 4—*Acroneuria abnormis* (Newman) was collected during supplemental sampling in 1991–1992; 5—probably *Cultus* sp.; 6—reported by Nelson (1957) as *Nemoura* sp.; 7—includes *Paragnetina immarginata* (Say) and *Paragnetina media* (Walker); 8—includes *Cheumatopsyche etrona* (Ross), *Hydropsyche betteni* (Ross), *Hydropsyche rossi* (Flint, Voshell, & Parker), *Hydropsyche sparna* (Ross), and *Hydropsyche venularis* (Banks); 9—includes *Ochrotrichia* sp.; 10—includes *Macronychus glabratus* (Say), *Optioservus* sp., *Promoresia elegans* (LeConte), and *Stenelmis* sp.; 11—includes *Brillia* sp., *Cardiocladius* sp., *Corynoneura* sp., *Cricotopus* spp., *Cryptochironomus* spp., *Glyptotendipes* sp., and *Polypedilum* spp. (Nelson 1957); 12—includes *Pentaneura* sp. and *Procladius* sp. (Nelson 1957); 13—excluded from NCBI analysis.

Taxa	TV	1956–1957	1991–1992
Ephemeroptera			
Ameletus lineatus (Traver)	2.1		X
Baetidae	5.2	X	X[1]
Caenis sp.	7.6	X	X
Epeorus spp.	1.2		X
Ephemerellidae	2.7	X	X[2]
Isonychia sp.	3.8		X
Stenonema spp.	7.1	X	X[3]
Tricorythodes sp.	5.4	X	
Odonata			
Argia sp.	8.7	X	
Plecoptera[4]			
Agnetina flavescens (Walsh)	0.0		X
Amphinemura sp.	3.4		X
Isogenus sp.	1.6	X[5]	
Isoperla sp.	5.5	X	
Shipsa rotunda (Claassen)	0.3	X[6]	X
Neoperla sp.	1.6		X
Paragnetina spp.	1.7		X[7]
Perlesta placida (Hagen)	4.9	X	X
Pteronarcys dorsata (Say)	1.7	X	X
Strophopteryx sp. (=*Brachyptera*)	2.5	X	X
Taeniopteryx maura (Pictet)	6.3	X	X
Megaloptera			
Corydalus cornutus (L.)	5.6	X	X
Nigronia serricornis (Say)	5.5		X
Trichoptera			
Agraylea sp.	6.2	X	
Glossosomatidae	1.5		X
Hydropsychidae	5.3	X	X[8]
Hydroptilidae	6.2	X	X[9]
Lepidostoma sp.	1.0		X
Lype diversa (Banks)	4.3		X
Nectopsyche exquisita (Walker)	3.8	X	X
Rhyacophila sp.	0.8		X
Hemiptera	8.8	X	
Coleoptera			
Anecaena sp.	7.9	X	
Berosus sp.	8.6	X	
Elmidae	5.4	X	X[10]
Gyrinus sp.	6.3	X	
Haliplus sp.	8.5	X	
Helophorus sp.	7.9	X	
Hydrochus sp.	7.9	X	
Unknown Hydrophilidae	7.9	X	
Diptera			
Antocha sp.	4.6		X
Ceratopogonidae	6.8	X	
Chelifera sp.	8.1		X
Chironomidae (non-Tanypodinae)	6.5	X[11]	X
Chironomidae (Tanypodinae)	6.5	X[12]	X
Dolichopodidae	9.7	X	
Hemerodromia sp.	8.1	X	X
Muscidae	7.0	X	
Simuliidae	6.8	X	X
Tipula spp.	7.7	X	X
Cnidaria (*Hydra* sp.)[13]	—	X	
Turbellaria	7.5	X	X
Nematoda	8.2	X	X
Mollusca			
Ancylidae (*Ferrissia* sp.)	6.9	X	X
Elimia sp. (=*Goniobasis*)	2.5	X	X
Somatogyrus alcoviensis? (Krieger)	2.5		X
Sphaeriidae	7.7		X
Corbicula fluminea (Müller)[13]	6.3		X
Annelida			
Oligochaeta	8.1	X	X
Hirudinea	8.2	X	X
Hydracarina	5.7	X	X
Cladocera[13]	—	X	X
Copepoda[13]	—	X	X

paired *t*-test) below the hydrophyte overstory and ranged from 0 to 0.8 m s^{-1} (mean, 0.4 m s^{-1}).

Daily water temperatures from the Middle Oconee River reflected a clear seasonal pattern throughout the study period (13 August 1991 to 12 August 1992, Fig. 3A), and ranged from 20 to 29°C in summer months and 5 to 18°C in winter. River discharge was generally higher in winter and spring than summer and autumn; however, the Middle Oconee exhibited a series of spates that did not always follow seasonal trends (Fig. 3B). Of two spates which exceeded 50 $m^3 s^{-1}$, one occurred 3 July 1992, during an otherwise low-flow period. Mean monthly standing crops of *P. ceratophyllum* on bedrock outcrops generally ranged from 376 to 587 g AFDM m^{-2} (Fig. 3C), except for November (1,045 g AFDM m^{-2}) and March (297 g AFDM m^{-2}). Unlike temperature and discharge, no seasonal trends were evident for *P. ceratophyllum* standing crops (Fig. 3C, Table 2).

Seasonal trends were not apparent for macroinvertebrate standing stocks and no significant differences were detected between total seasonal abundances or total seasonal biomass values (Table 3). For individual functional

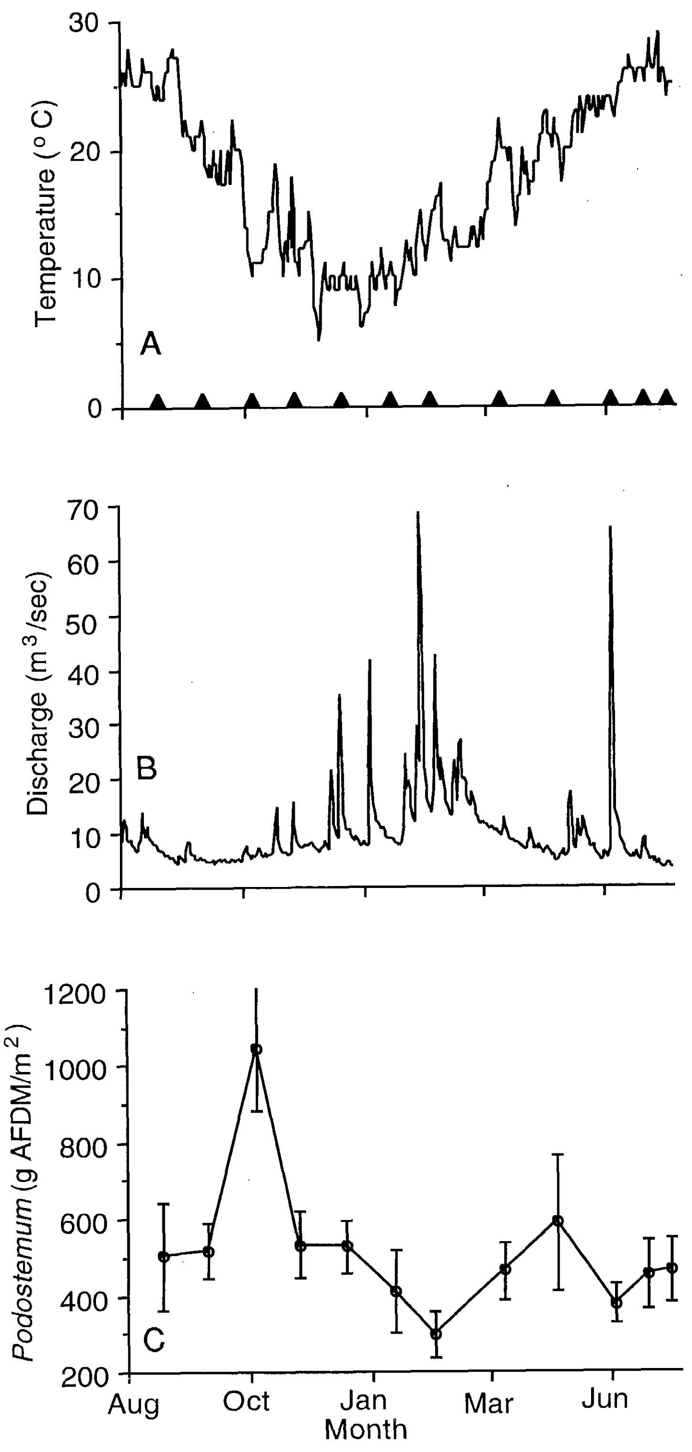

Fig. 3. Daily physical parameters of water temperature (A) and discharge (B) and monthly standing crops of *Podostemum ceratophyllum* (C) for the 1991–1992 study period (13 August 1991–12 August 1992). Benthic sampling dates are indicated by triangles along the water temperature abscissa.

Table 2. Seasonal standing-crop biomass of *Podostemum ceratophyllum* on bedrock outcrops. Values are expressed as means ±1 SD. Sheffé multiple range test detected no significant differences between seasonal values ($P > 0.138$).

Season	*n*	Biomass (g AFDM m^{-2})
Autumn	14	700.5±383.0
Winter	15	489.0±192.2
Spring	14	470.4±226.2
Summer	15	430.2±42.6

groups, seasonal abundances were occasionally significantly higher (i.e. collector-filterers in autumn) or lower (scrapers in summer), as were biomass values (higher for collector-gatherers in spring and shredders in winter), but again no trends were apparent. Rather, total macroinvertebrate abundance and biomass were significantly correlated to standing crops of *P. ceratophyllum,* as were abundances and biomass values for all functional groups except shredders (Table 4).

On an annual basis, mean abundances were highest for scrapers, collector-gatherers, and collector-filterers, lower for predators, and lowest for shredders (Table 5). Scrapers and collector-filterers also constituted the greatest mean annual biomass, but collector-gatherer biomass was not significantly different from shredder and predator biomass.

Total annual macroinvertebrate production on the bedrock outcrop was 181.9 g AFDM m^{-2} yr^{-1} (Table 6). Collector-filterers accounted for the greatest proportion of annual production (63%), followed by scrapers (18%), predators (7%), and collector-gatherers and shredders (each 6%). Several taxa within each functional group contributed substantially to total production. These included *Hydropsyche* spp. and *Cheumatopsyche* spp. (57% combined), the hydrobiid snail *Somatogyrus* sp. (13%), and the introduced Asian clam *Corbicula fluminea* Müller (6%). Taxa that accounted for >0.5% annual functional-group production are listed in Table 6.

Physical parameters measured in 1991–1992 were very similar to those of the 1956–1957 study period (5 April 1956–4 April 1957). Seasonal temperature trends in 1956–1957 ranged from 21 to 27°C in summer and from 4 to 14°C in winter. Discharge was again higher in winter and spring than summer and autumn. Three spates exceeded 50 m^3 s^{-1} in the 1956–1957 study period: two in spring and one in July during an otherwise low-flow period. As in 1991–1992, standing crops of *P. ceratophyllum* exhibited no seasonal trends in 1956–1957 (Nelson and Scott 1962), and measures of annual apparent hydrophyte productivity were similar (Table 7). Mean annual water temperature, discharge, and *P. ceratophyllum* standing crops were slightly higher in 1991–1992, but no significant differences were detected between daily temperature and discharge values (paired *t*-test, $P > 0.50$) or mean annual macrophyte standing crops (pooled *t*-test, $P > 0.50$).

Taxonomic composition of the macroinvertebrate community differed greatly between the 1956–1957 and 1991–1992 studies. Although total number of taxa collected were similar (45 in 1956–1957, 42 in 1991–1992), only 27 taxa were common to both studies (Table 1). Notable additions in 1991–1992 included *Somatogyrus* sp., which accounted for most of scraper abundance, bio-

Table 3. Seasonal standing-stock abundance (individuals $m^{-2} \times 10^3$) and biomass (g AFDM m^{-2}) for benthic functional composition on bedrock outcrops. Seasonal values are expressed as means ±1 SD; significant differences among means are based on $\log_{10}(X + 1)$-transformed values and indicated by different superscript letters (Sheffé multiple range test, $P = 0.05$).

	n	Scrapers	Collector-gatherers	Shredders	Collector-filterers	Predators	Total
Abundance							
Autumn	14	21.5±11.2^{ab}	19.0±17.2^{a}	1.2±1.7^{a}	28.9±17.1^{a}	3.5±4.1^{a}	74.0±37.6^{a}
Winter	15	16.9±16.4^{a}	21.8±20.9^{a}	1.4±1.3^{a}	9.9±7.4^{b}	2.8±2.6^{a}	52.9±30.0^{a}
Spring	14	21.3±18.3^{ab}	34.5±21.4^{a}	1.4±1.5^{a}	9.4±8.0^{b}	4.4±6.6^{a}	71.0±45.6^{a}
Summer	15	32.5±16.1^{b}	10.1±6.8^{a}	0.6±0.8^{a}	11.9±7.7^{b}	1.9±1.4^{a}	57.0±20.0^{a}
Biomass							
Autumn	14	8.6±6.9^{a}	0.6±0.5^{a}	1.7±3.8^{a}	10.8±6.0^{a}	4.1±7.0^{a}	25.8±11.1^{a}
Winter	15	10.1±9.9^{a}	0.5±0.5^{a}	8.9±11.4^{b}	6.4±6.6^{a}	2.0±3.5^{a}	27.8±21.8^{a}
Spring	14	8.9±6.0^{a}	4.0±3.9^{b}	0.3±0.4^{a}	8.6±9.1^{a}	3.3±2.8^{a}	25.0±18.8^{a}
Summer	15	4.9±3.2^{a}	0.4±0.2^{a}	0.6±1.0^{a}	4.1±3.1^{a}	2.7±4.2^{a}	12.7±7.6^{a}

mass, and production in this study, the trichopteran shredder *Lepidostoma* sp., predaceous perlid stoneflies *Agnetina flavescens* (Walsh) and *Paragnetina* spp., and the bivalve *C. fluminea*. Taxa present in 1956–1957 but not in 1991–1992 included the tricorythid mayfly *Tricorythodes* sp. and predaceous coleopterans and dipterans (Table 1).

Functional group abundance and biomass differed radically between studies. Except for scrapers, macroinvertebrate abundances were lower in 1991–1992 than in 1956–1957 (Fig. 4A), and total abundance was ~40% less in 1991–1992. Conversely, biomass was much greater for all functional groups in 1991–1992, most notably for shredders which were ~16-fold greater (Fig. 4B), and total macroinvertebrate biomass was ~4× greater in 1991–1992 than in 1956–1957. Mean individual macroinvertebrate biomass (functional group biomass / functional group abundance) was greater in 1991–1992 than in 1956–1957, especially for shredders which showed a 40-fold increase (Fig. 4C). For total macroinvertebrates, mean individual biomass was ~7× greater in 1991–1992 than in 1956–1957.

Indices of biotic integrity provided mixed results of comparative stream condition between 1956–1957 and 1991–1992. Total taxa richness was similar between studies, as was percent abundance of the dominant taxon (Table 8). However, the number of EPT taxa was significantly higher in 1991–1992 and the NCBI score was significantly lower than calculated for 1956–1957 data. The latter two parameters indicate improved biotic integrity in 1991–1992 vs. 1956–1957.

Discussion

Factors which influence macroinvertebrate community structure and function include water temperature (Sweeney 1984), stream discharge (Ward 1984), riparian vegetation (Ward 1984), and substratum constituency (Minshall 1984). Long-term records for the study area indicate water temperature and discharge regimes were very similar during the 1956–1957 and 1991–1992 studies (Table 7). Physical descriptions and photographs of the site (Fig. 1; Nelson 1957; Nelson and Scott 1962), and comparisons of monthly standing crops of *P. ceratophyllum* (Table 7)

Table 4. Correlation of benthic functional group abundance and biomass to standing crops of *Podostemum ceratophyllum* (g AFDM m^{-2}). Comparisons are based on simple linear correlations of $\log_{10}(X + 1)$-transformed values ($n = 58$) and are expressed in terms of correlation coefficient (r) and probability value (P). Asterisks: *—significant correlation ($P < 0.05$).

Functional group	*r*	*P*
Macroinvertebrate abundance (individuals m^{-2})		
Scrapers	0.278	0.0349*
Collector-gatherers	0.361	0.0054*
Shredders	0.156	0.2436
Collector-filterers	0.452	0.0004*
Predators	0.277	0.0352*
Total abundance	0.504	0.0001*
Macroinvertebrate biomass (g AFDM m^{-2})		
Scrapers	0.354	0.0064*
Collector-gatherers	0.280	0.0335*
Shredders	0.197	0.1390
Collector-filterers	0.521	0.0001*
Predators	0.364	0.0050*
Total biomass	0.496	0.0001*

Table 5. Annual abundance (individuals $m^{-2} \times 10^3$) and biomass (g AFDM m^{-2}) of benthic functional groups on the bedrock-outcrop habitat. Values are expressed as means ±1 SD ($n = 58$). Differences among means are based on transformed values [$\log_{10}(X + 1)$] and indicated by different superscript letters (Scheffé multiple range test, $P = 0.05$).

Functional group	Abundance	Biomass
Scrapers	22.8±16.4^{a}	8.0±7.0^{a}
Collector-gatherers	21.2±19.2^{a}	1.4±2.4^{b}
Shredders	1.1±1.8^{b}	2.8±7.0^{b}
Collector-filterers	14.6±13.2^{a}	7.3±6.8^{a}
Predators	3.2±4.1^{c}	3.0±4.6^{b}
Annual total	62.9±34.6	22.4±16.6

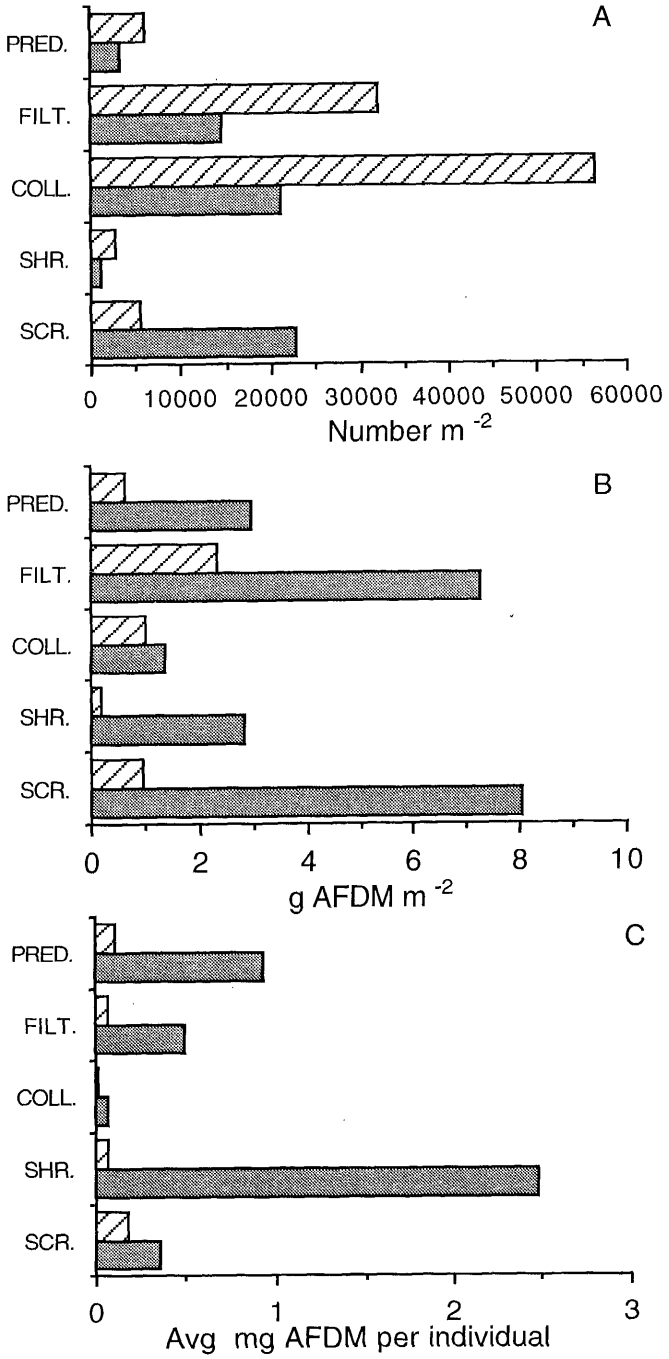

Fig. 4. Benthic functional-group abundances (A), biomass (B), and average mass per individual macroinvertebrate (C) in 1956–1957 (hatched, Nelson 1957) and 1991–1992 (shaded, this study) on bedrock-outcrop habitat. Functional-group designations are: PRED.—predators; FILT.—collector-filterers; COLL.—collector-gatherers; SHR.—shredders; and SCR.—scrapers.

suggest little physical or structural change has taken place in the shoals or associated riparian corridor. It is unlikely that these physical parameters account for differences in macroinvertebrate community structure observed between studies.

Table 6. Standing-stock abundance (*A*, individuals $m^{-2} \times 10^3$), biomass (*B*, g AFDM m^{-2}), and production (*P*, g AFDM m^{-2} yr^{-1}) of functional groups and major faunal taxa on the bedrock-outcrop habitat in 1991–1992. Taxa that contributed >0.5% of functional group production are included. Insect order designations are: C—Coleoptera; D—Diptera; E—Ephemeroptera; M—Megaloptera; P—Plecoptera; T—Trichoptera.

Taxon	Insect order	*A*	*B*	*P*
Scrapers				
Somatogyrus sp.	—	17.3	6.4	24.3
Baetis spp.	E	38.2	0.3	3.7
Elimia sp.	—	0.1	0.9	3.7
Stenonema spp.	E	1.0	0.1	0.6
Heterocloeon sp.	E	0.3	<0.1	0.5
Stenelmis sp.	C	0.4	<0.1	0.2
Others	—	<0.1	<0.1	0.1
Total		22.8	7.8	33.1
Shredders				
Pteronarcys sp.	P	<0.1	2.3	7.7
Tipula spp.	D	<0.1	0.5	2.2
Lepidostoma sp.	T	1.0	<0.1	0.3
Others	—	0.1	<0.1	<0.1
Total		1.1	2.8	10.2
Collector-gatherers				
Serratella spp.	E	5.8	0.9	5.8
Chironomidae	D	11.1	0.1	3.0
Ephemerella spp.	E	0.5	0.2	1.3
Oligochaeta	—	3.3	0.1	0.3
Others	—	0.5	<0.1	0.1
Total		21.2	1.4	10.5
Collector-filterers				
Hydropsyche spp.	T	10.0	5.5	92.8
Cheumatopsyche spp.	T	4.0	0.8	10.5
Corbicula sp.	—	0.1	0.9	10.2
Simulium spp.	D	0.5	<0.1	0.6
Others	—	<0.1	0.1	0.4
Total		14.6	7.3	114.5
Predators				
Corydalus sp.	M	<0.1	1.7	6.7
Paragnetina sp.	P	0.5	0.8	4.4
Agnetina sp.	P	0.3	0.4	2.4
Turbellaria	—	0.3	<0.1	0.1
Others	—	2.1	<0.1	0.1
Total		3.2	3.0	13.6
Total macroinvertebrates		62.9	22.2	181.9

In general, no seasonal trends were evident in macroinvertebrate standing stocks in 1956–1957 (Nelson and Scott 1962) or 1991–1992 (Table 2). Benthic abundances and biomass in 1991–1992 were correlated to standing crops of *P. ceratophyllum*, especially for collector-filterers (Table 3), which consisted primarily of hydropsychid caddisflies (Table 6). In Piedmont streams, rock outcrops covered by *P. ceratophyllum* generally support higher densities of hydropsychids (Caldwell 1973) than outcrops without macrophytes (Freeman and Wallace 1984; *but see* Parker and Voshell 1983). *P. ceratophyllum* provides

Table 7. Comparisons of physical and hydrophyte parameters in 1956–1957 (Nelson 1957; Nelson and Scott 1962) and 1991–1992 (this study). No significant differences were detected for temperature or discharge parameters (paired *t*-test, $P > 0.50$), or for *Podostemum ceratophyllum* biomass (pooled *t*-test, $P > 0.50$).

Parameter	5 Apr 56–4 Apr 57		13 Aug 91–12 Aug 92	
	Mean ± SE	Range	Mean ± SE	Range
Temp. (°C)	17.9±0.3	3.9–27.2	18.6±0.3	5.0–28.9
Annual degree-days (°C)	6,187		6,443	
Discharge (m^3 s^{-1})	8.9±0.4	0.9–59.4	9.9±0.4	3.3–68.5
P. ceratophyllum biomass				
Standing crop (g AFDM m^2)	350.2±33.8	136.8–635.0	514.0±53.2	
Apparent productivity (g AFDM m^{-2} yr^{-1})	930		907	296.8–1,044.8

attachment sites and refugia for hydropsychids (Parker and Voshell 1983; Freeman and Wallace 1984) while affording access to microhabitats of high current velocities with increased delivery rates of entrained food resources (Cudney and Wallace 1980).

Benthic production for the Middle Oconee River shoals was estimated to be 181.9 g AFDM m^{-2} yr^{-1}, which is in the upper range of production values for studies cited by Benke (1993). Two factors may account for substantially higher production estimates than normally encountered. Most existing production studies (>85%) are from streams with discharge < 10 m^3 s^{-1} (Benke 1993); relatively little is known about levels of secondary production in rivers the size of the Middle Oconee. Also, this production estimate accounts for only bedrock-outcrop habitat and does not include extensive reaches of shifting sand also common to Piedmont rivers. Similar to snag habitat in the sandy-bottomed Ogeechee River of the Georgia Coastal Plain (Benke et al. 1984), bedrock outcrops of the Middle Oconee represent limited stable substratum in an otherwise unstable river-bottom. These habitats support high macroinvertebrate production, generally dominated by collector-filterers which remain sessile on stable substrata and utilize river current to supply entrained food resources (Cudney and Wallace 1980).

The high proportion of collector-filterer production (63%) in the Middle Oconee is not uncommon for rivers of this size. Benke (1993) plotted relative contributions of functional-group production for 19 streams, using discharge as a measure of stream size. Rivers with discharge ~10 m^3 s^{-1} generally had strong collector-filterer components to secondary production. High proportions of collector-filterers have also been found associated with *P. ceratophyllum* substrata in the New River (West Virginia; Voshell and Parker 1985).

Scraper production, which accounted for the second largest contribution to total benthic production in the Middle Oconee (18%), was dominated by the hydrobiid snail, *Somatogyrus* sp., which grazes on aufwuchs associated with *P. ceratophyllum* (Krieger 1972). These snails most likely represent *Somatogyrus alcoviensis* (Krieger), first described in shoaled reaches of the Yellow and Alcovy Rivers of the Altamaha River system (Krieger 1972).

Nelson and Scott (1962) estimated annual secondary production for the Middle Oconee site in 1956–1957 to be 37.8 g AFDM m^{-2} yr^{-1}. This estimate was based on calculations of net apparent production—the same procedure used for *P. ceratophyllum* productivity estimates—and cannot be directly compared to production estimates from the present study. To ascribe a more comparable value to secondary production in 1956–1957, we multiplied mean annual biomass of individual taxa in 1956–1957 by *P:B* ratios for the same taxa from 1991–1992. Taxa unique to 1956–1957 were assigned a conservative *P:B* of 5 (note: unique taxa contributed relatively little to total biomass in 1956–1957). From this approach we estimated secondary production in 1956–1957 to be half the 1991–1992 value (90 g AFDM m^{-2} yr^{-1}) and dominated by collector-filterers (66 g AFDM m^{-2} yr^{-1}) and collector-gatherers (18 g AFDM m^{-2} yr^{-1}),

Table 8. Comparative indices of biotic integrity for the macroinvertebrate communities of the bedrock-outcrop habitat in 1956–1957 (Nelson 1957) and 1991–1992 (this study). Indices are presented as means of monthly samples ±1 SD. No significant differences were detected for total taxa richness (pooled *t*-test, $P > 0.10$) and percent contribution of dominant taxon (pooled *t*-test, $P > 0.50$). Significant differences were detected for the NCBI (Mann-Whitney, $P < 0.001$) and EPT (pooled *t*-test, $P < 0.001$) indices.

Biotic index	1956–1957	1991–1992
Total taxa richness	20±4	22±3
Percent contribution of dominant taxa	36±17	33±11
Modified NCBI	6.66±0.20	4.63±0.50
Number of EPT taxa	7±2	11±2

as opposed to filterers and scrapers in 1991–1992 (Table 6). Although secondary production was almost assuredly higher in 1991–1992 than in 1956–1957, production estimates based on *P:B* only approximate those based on size-frequency and community-level methods. Further comparative interpretations of secondary production estimates between study periods are inappropriate.

Comparisons of macroinvertebrate taxonomic composition, abundance, and biomass indicate major differences in community structure between the 1956–1957 and 1991–1992 studies. The most obvious change in taxonomic composition was *Somatogyrus.* Although none were reported in 1956–1957 (Nelson 1957; Nelson and Scott 1962), it was the dominant taxon in 1991–1992 in terms of abundance and biomass (Table 6). Krieger (1972) reported *S. alcoviensis* was absent from silt-laden habitats, and the occurrence of *Somatogyrus* in 1991–1992 but not in 1956–1957 suggests silt loads may have decreased. High densities of *Somatogyrus* in 1991–1992 may also account for decreases in other taxa, such as some Chironomidae and *Elimia* sp. Mulholland and Lenat (1992) noted that Piedmont streams with large numbers of *Elimia* generally support low numbers of grazing chironomids, suggesting a possible competitive interaction. Because of its small size, *Somatogyrus* might be even more efficient than *Elimia* at scraping the thinly dissected surfaces of *P. ceratophyllum* stems and leaves, providing a further competitive advantage in bedrock-outcrop habitat, which helps explain absolute reductions in both chironomid and *Elimia* standing stocks in the 1991–1992 study.

C. fluminea was another dominant taxon in 1991–1992 not found in 1956–1957. *C. fluminea* was first discovered in the Altamaha River in 1971 and has since spread throughout the basin, primarily in areas of mud and sand substrata (Gardner et al. 1976). The presence of *C. fluminea* on bedrock-outcrop habitat is likely facilitated by the *P. ceratophyllum* overstory, which significantly reduces mean current velocity, thereby lessening potential scouring and displacement of clams.

With the exception of scrapers, which were strongly influenced by the *Somatogyrus* population, a fundamental change in community structure between 1956–1957 and 1991–1992 was reduction in mean functional group abundance and increase in biomass, indicating a shift from smaller to larger bodied taxa (Fig. 4C). In 1956–1957, collector-gatherer biomass consisted mainly of chironomids and oligochaetes (Nelson 1957); in 1991–1992, larger ephemerellid mayflies (*Serratella* spp. and *Ephemerella* spp.) accounted for most of collector-gatherer biomass (Table 6). Similarly, shredder biomass in 1956–1957 was dominated by a small taeniopterygid plecopteran, *Taeniopteryx maura* Pictet (Nelson 1957); in 1991–1992, larger shredders such as *Pteronarcys dorsata* Say and *Tipula* spp. were abundant and mean individual shredder biomass increased over 40-fold (Fig. 4C). Microfilterers (i.e. Diptera: Simuliidae) accounted for >90% of collector-filterer abundance and biomass in 1956–1957 (Nelson 1957), but in 1991–1992 simuliid densities were reduced and filterer biomass and abundance was dominated by macrofilterers (i.e. hydropsychids, Table 6). Trends in invertebrate predators followed those of primary consumers; small taxa that dominated in 1956–1957 (e.g. Hydracarina and *Perlesta placida* Hagen; Nelson 1957) were replaced by larger taxa in 1991–1992 (e.g. *Paragnetina* spp., *A. flavescens,* and *Corydalus cornutus* L.; Table 6).

A shift from smaller or larger bodied taxa suggests a reduction in stream contaminants between the two studies. Smaller bodied, multivoltine taxa with relatively short life-cycles have been shown to persist and dominate benthic community composition in stream systems subjected to pesticide disturbances (Lugthart and Wallace 1992). These taxa are able to rapidly recolonize and develop between pesticide applications, and short generation times may facilitate development of population-level resistance to toxicants (Heckman 1981).

At first interpretation, comparisons of mean indices of biotic integrity between 1956–1957 and 1991–1992 produced mixed results (Table 8). Total taxa richness and percent contribution of the dominant taxon showed no significant change between studies, while numbers of EPT taxa and NCBI indicated significant improvement of biotic integrity in 1991–1992. Two factors may have limited the effectiveness of total taxa richness and percent dominant taxon as indices of biotic integrity. First was the highly conservative nature of taxonomic identifications used for study comparisons. Conservatism was necessary to prevent interpreting changes in systematics as changes in community composition, but it reduced and equalized the total number of taxa reported by both studies. Second, taxonomic composition between 1956–1957 and 1991–1992 shifted as organisms tolerant to perturbation were replaced by a similar number of less tolerant taxa in 1991–1992 (Table 8). Taxonomic composition was more dynamic than total richness. Although percent of dominant taxon did not change, dominance did shift from simuliids in 1956–1957 to *Somatogyrus* sp. and hydropsychids in 1991–1992. In relatively unimpacted rivers of southeastern U.S., species composition, diversity, and functional organization of *P. ceratophyllum* habitat is dominated by hydropsychids (Caldwell 1973). Thus by definition (Karr and Dudley 1981), shift in dominance from simuliids to hydropsychids indicates an improvement in stream biotic integrity. Remaining indices (EPT and NCBI), which were less influenced by conservative taxonomic classifications and unobscured by taxonomic shifts, also indicated significant improvement of biotic integrity in 1991–1992 relative to 1956–1957. We conclude stream condition of the river had improved over the 35-yr interim period.

Land-use practices in the Piedmont region prior to and during the 1950s undoubtedly stressed the aquatic biota. Cotton and corn row-cropping of hill terrain greatly increased soil erosion and suspended sediment inputs to streams and rivers (Mulholland and Lenat 1992). In 1956–1957, Nelson (1957) reported silt was an obvious pollutant, and heavy silt loads seriously limited light penetration and the development of algal populations (Nelson and Scott 1962). Crop protection strategies in the 1950s called for the liberal use of pesticides to control insect damage (U.S. Dep. Agriculture 1952). This was especially true for cotton (Pimentel and Levitan 1986), and farmers were routinely advised to apply an extensive array of toxins which included benzene hexachloride, chlordane, DDT, and toxaphene (U.S. Dep. Agriculture 1952). Significant quantities of pesticides inevitably ended up in aquatic habitats either through leaching or, as with DDT and toxaphene, associated with suspended-sediment loads (Pimentel and Levitan 1986).

Agriculture ceased to be a major activity in the catchment by the mid-1970s, and cotton and corn row-cropping were virtually nonexistent by 1980 (Fig. 2). Subsequently, excessive sediment loads which had been described by Nelson (1957) were noticeably absent during the 1991–1992 study; the river is still turbid during high-flow conditions, but substratum becomes clearly visible to maximum depths in the shoals during mean and low-flow periods. Furthermore, general usage of agricultural chemicals in the basin has greatly diminished over the last three decades. In 1964 pesticides were applied over 1,240 ha in Barrow, Clarke, and Jackson counties; application in 1987 was limited to <380 ha (U.S. Dep. Commerce 1910–1988).

Changing land-use practices in the catchment is potentially the key factor in improved biotic integrity of the river. Decreased sediment loads allow for increased light penetration and periphyton development, facilitating greater scraper abundance and biomass in 1991–1992 relative to 1956–1957. Reduction of inorganic suspended sediment also improves overall seston quality (Voshell and Parker 1985), providing a better food resource for macrofilterers, which also increased in abundance and biomass in 1991–1992. Finally, the shift in community composition from small, multivoltine taxa to larger, longer lived invertebrates (including intolerant EPT taxa) suggests reductions in contaminants and improvement of streamwater quality.

Ward (1975) noted riparian vegetation at the North St. Vrain Creek study site had changed over 29 yr, but land use in the catchment had not. Subsequently, taxonomic composition of the benthic community was similar between studies. Conversely, our study showed land-use patterns in the Middle Oconee River had changed since the Nelson and Scott (1962) study, but in-stream habitat and riparian vegetation at the study site remained similar. Macroinvertebrate community structure, function, and biotic integrity of the Middle Oconee shoals were quite different between studies. We conclude that land-use practices in the catchment exert a fundamental influence on the lotic ecosystem; water resource management plans which focus on instream and short stretches of riparian habitats but do not address basinwide land use are limited in their ability to enhance and sustain water quality and condition of the stream resource.

Our study indicates an improvement in the condition of the Middle Oconee River as agricultural perturbations have diminished in the latter 20th century. However, increasing urbanization throughout the region is becoming a major influence on water resources of the Piedmont province (Mulholland and Lenat 1992). Future studies may detect a reversal in stream condition as urbanization increases.

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