J. N. Am. Benthol. Soc., 2004, 23(4):713–727
© 2004 by The North American Benthological Society

# Role of *Podostemum ceratophyllum* Michx. in structuring benthic macroinvertebrate assemblages in a southern Appalachian river

JOHN J. HUTCHENS, JR.[1] AND J. BRUCE WALLACE[2]
*Institute of Ecology, University of Georgia, Athens, Georgia 30602 USA*

ERIC D. ROMANISZYN[3]
*Department of Entomology, University of Georgia, Athens, Georgia 30602 USA*

*Abstract.* *Podostemum ceratophyllum* Michx. has been associated with extremely high secondary production of benthic macroinvertebrates in open-canopy rapids. We conducted an experiment in the 7th-order Little Tennessee River, North Carolina, to test whether varying amounts of *Podostemum* influenced macroinvertebrate abundance, biomass, community composition, and functional feeding group structure. The experiment consisted of 3 treatments in which *P. ceratophyllum* was completely, partially, or not removed from portions of 4 bedrock outcrops at 2 sites. Macroinvertebrates were sampled at 0, 3, and 6 wk post treatment. Complete removal of *P. ceratophyllum* greatly reduced overall macroinvertebrate abundance and biomass and altered assemblage structure, but had relatively little effect on functional structure. The lack of change in functional feeding group structure was probably a result of the importance of *P. ceratophyllum* as a substrate for epiphytic algae, and the availability of nearby colonists in undisturbed habitats. We found a strong positive relationship between surface area of *Podostemum* and total macroinvertebrate abundance and biomass. We estimated that *P. ceratophyllum* increased surface area by 3 to 4 times over bare bedrock. *Podostemum ceratophyllum* in the Little Tennessee River serves as an important habitat supporting high abundance and biomass of macroinvertebrates.

*Key words:* macrophytes, productivity, habitat, surface area, functional feeding groups, filterers, gatherers, scrapers.

Substratum is one of the major factors influencing stream macroinvertebrate distribution and productivity (Hynes 1970, Minshall 1984, Allan 1995), and the presence of aquatic vegetation can have a profound effect on the benthic fauna (Percival and Whitehead 1929). Aquatic plants increase available habitat for macroinvertebrates by augmenting surface area (e.g., Cattaneo and Kalff 1980), alter local hydrology by decreasing current velocity (e.g., Sand-Jensen 1998, Madsen et al. 2001, Dodds and Biggs 2002), enhance streambed stability (e.g., Fritz and Feminella 2003), and provide food resources. Food effects can be either direct consumption (= herbivory; e.g., Lodge 1991, Jacobsen and Sand-Jensen 1992) or indirect through enhanced surface area for epiphytic algae (e.g., Cattaneo and Kalff 1980, Gregg and Rose 1982) and increased deposition of detritus (e.g., Gregg and Rose 1982, Sand-Jensen 1998). Aquatic macrophytes in fast-flowing streams are typically restricted to slower-flowing habitats (e.g., *Justicia americana* (L.) Vahl). One notable exception, however, is the Podostemaceae, which thrive in open-canopy rapids (e.g., Everitt and Burkholder 1991). Although the Podostemaceae is primarily a tropical family (Philbrick and Novelo 1995), one species, *Podostemum ceratophyllum* Michx., is found in the eastern US (Philbrick and Crow 1983) where it provides a diverse, 3-dimensional habitat for macroinvertebrates (Nelson and Scott 1962, Parker and Voshell 1983). In fact, secondary production of filter feeders in *P. ceratophyllum*-covered habitats (Grubaugh and Wallace 1995, Grubaugh et al. 1997) is among the highest ever recorded for streams (Huryn and Wallace 2000).

Grubaugh et al. (1997) found extremely high productivity of macroinvertebrates in *Podostemum*-covered habitats in the Little Tennessee River, North Carolina. Our overall goal was to investigate whether varying amounts of *P. cera-*

[1] Present address: Department of Biology, Coastal Carolina University, P.O. Box 261954, Conway, South Carolina 29528-6054 USA.
E-mail: jjhutche@coastal.edu
[2] E-mail address: bwallace@uga.edu
[3] Present address: Science Applications International Corporation, 151 Lafayette Dr., Oak Ridge, Tennessee 37831 USA. E-mail: eric.d.romaniszyn@saic.com

TABLE 1. Physical characteristics of Iotla and Needmore sites on the Little Tennessee River (data from Grubaugh et al. 1997 except velocity and temperature).

| Parameter | Iotla | Needmore |
|---|---|---|
| Distance from headwater (km) | 38 | 67 |
| Catchment area (ha) | 83,660 | 112,900 |
| Elevation (m above sea level) | 597 | 540 |
| Water-surface slope (%) | 0.14 | 0.35 |
| Mean annual discharge ($m^3/s$) | 22.18 | 29.54 |
| Mean velocity (m/s) | | |
| Week 0 | 0.80 | 0.79 |
| Week 3 | 0.48 | 0.63 |
| Week 6 | 0.61 | 0.54 |
| Mean bankfull width (m) | 60 | 70 |
| Mean bankfull depth (cm) | 50 | 50 |
| Habitat proportions (%) | | |
| Depositional | 35 | 28 |
| *Podostemum*-covered cobble riffle | 27 | 0 |
| *Podostemum*-covered bedrock outcrop | 38 | 72 |
| Mean daily temperature (°C) (8-y record)[a] | – | 13.6 |
| Mean annual degree days (8-y record)[a] | – | 4970 |
| Mean daily temperature (°C) during experiment | – | 22.7 |

[a] Based on temperatures from 2-h interval thermistor recordings at Needmore only

*tophyllum* influenced macroinvertebrate abundance and biomass. We conducted an experiment at 2 of the sites previously studied by Grubaugh et al. (1997) in which we removed either all *P. ceratophyllum* or all but the basal 2 cm, and followed macroinvertebrate colonization for 6 wk. *Podostemum* forms a thick mat on stable substrates, and may also form long (>15 cm) stems during summer. Our treatments were, therefore, designed to show how removing the entire plant or just the long stems influenced macroinvertebrates. Specifically, we assessed how *P. ceratophyllum* removal influenced: 1) abundance and biomass of total macroinvertebrates, each functional feeding group (FFG), and individual taxa, 2) proportion of total abundance and biomass comprised by each FFG, and 3) community composition. We hypothesized that complete removal of *P. ceratophyllum* would dramatically reduce total macroinvertebrate abundance and biomass because of habitat loss. Further, we expected filter feeders to decline and scraper abundance and biomass to increase because of habitat loss and enhanced algal colonization on newly opened bedrock, respectively. We also hypothesized that removal of all but the basal *P. ceratophyllum* would result in a decline in macroinvertebrate abundance and biomass but not change functional structure or community composition because of the maintenance of some habitat structure.

## Methods

### *Study sites*

We did the study in the Little Tennessee River, a 7th-order stream in the Blue Ridge Physiographic Province of the southern Appalachian Mountains (North Carolina, USA). Underlying geology includes highly weathered crystalline rock, which results in low ionic concentrations in stream water (Swank and Bolstad 1994). The 2 study sites, Iotla and Needmore (sites R-2 and R-3, respectively, of Grubaugh et al. 1997; lat 35°20′11″N, long 83°31′37″W), were downstream from the confluence of the Cullasaja River and the municipality of Franklin, North Carolina. Needmore was 29 km downstream of Iotla, and both sites had narrow, forested floodplains. In the study area, the river passed through the Nantahala National Forest, which contains scattered residences and agricultural fields. Habitats in both study sites were dominated by cobble riffles and bedrock outcrops with dense *P. ceratophyllum* growths (Table 1). Bedrock outcrops

extended across most of the river width at Needmore and in large blocks at Iotla. We determined discharge from a US Geologic Survey gauging station at Needmore and estimated discharge at Iotla from catchment area using linear regression after Grubaugh et al. (1996).

### Podostemum *removal experiment and surface area determination*

The experiment, done in the summer of 1997, consisted of 3 treatments in which we completely (SCRAPE), partially (SNIP), or did not (CONTROL) remove *P. ceratophyllum* from portions of 4 haphazardly chosen bedrock outcrops within a 100-m reach at each site. We removed all *P. ceratophyllum* from a 0.5625-$m^2$ area using putty knives and wire brushes for the SCRAPE treatment. In the SNIP treatment, we removed all *P. ceratophyllum*, except for the basal 2 cm, from a 0.5625-$m^2$ area using scissors. We did all treatments on each of the bedrock outcrops, with each treatment on each outcrop having similar flows and depths. We measured current velocity for each treatment on each date with a velocity-head rod (Wilm and Storey 1944). We began treatments and initial macroinvertebrate sampling on 15 July 1997; we repeated sampling 3 and 6 wk later. We did not sample the SCRAPE treatment on week 0 (i.e., the day we removed *P. ceratophyllum*) because visual and tactile inspection revealed no *P. ceratophyllum* or macroinvertebrates on the bedrock after *P. ceratophyllum* removal. Hence, we assumed macroinvertebrate abundance and biomass and *P. ceratophyllum* standing crop to be 0 for the SCRAPE treatment in Week 0.

We estimated the surface area provided by *P. ceratophyllum* at our study sites by calculating the surface area of separate parts of *P. ceratophyllum* collected from both sites. We measured stem, root, and apical tip length on a microscope fitted with an ocular micrometer, and calculated surface area of the parts using appropriate formulas depending on the shape of the part ($n$ = 6 plants). We also determined biomass (ash-free dry mass [AFDM]) for each part. We regressed biomass on surface area for each plant using untransformed data, and used this linear regression equation to predict the amount of surface area added by *P. ceratophyllum* at each site using mean standing crops in the CONTROL treatments. We also used this equation to estimate surface area of *P. ceratophyllum* in each of our samples, and correlated surface area with total macroinvertebrate abundance and biomass in each sample (see sampling methods below). We calculated Pearson product-moment correlations using $\log_{10}(x + 1)$-transformed data.

### Podostemum *and macroinvertebrate sampling*

We collected one sample from each treatment on each bedrock outcrop on each collection date using a modified T-sampler (English 1987). The T-sampler sampled a 103-$cm^2$ area and was fit with a 250-μm mesh catchnet. We firmly pressed the sampler against the bedrock so that the *P. ceratophyllum* mat formed a seal around the sampler. We scraped *Podostemum* and associated macroinvertebrates inside the sampler from the bedrock with a putty knife, and preserved all material in 6 to 8% formalin containing a small amount of phloxine-B dye to aid in sample processing (Mason and Yevich 1967).

In the laboratory, we washed samples through nested 1-mm and 250-μm mesh sieves. We oven dried *Podostemum* retained on the 1-mm sieve at 60°C, and weighed and ashed it at 500°C for 24 h to calculate AFDM. We processed fine benthic organic matter (FBOM) retained on the 250-μm mesh sieve similarly to calculate AFDM. However, we undoubtedly underestimated FBOM because most FBOM is strongly skewed to the smallest size fractions and may have passed through the sieve (e.g., Minshall et al. 1982).

We examined all material retained on the 1-mm sieve at 15× magnification to recover all macroinvertebrates, including careful inspection of macroinvertebrates attached to *P. ceratophyllum*. We subsampled material retained on the 250-μm sieve as necessary using a sample splitter (Waters 1969), and removed organisms under 15× magnification. We identified, counted, and measured all invertebrates to the nearest millimeter for conversion to AFDM using taxon-specific length–mass regressions (Benke et al. 1999). Taxonomic and FFG assignments followed those of Merritt and Cummins (1996). We identified most insects to genus with the exception of Chironomidae, Ceratopogonidae, Empididae, and Hydropsychidae. We enumerated the Chironomidae as either Tanypodinae or collector-gatherer Chironomidae. We identified Ceratopogonidae and Empididae to family. We combined hydropsychid genera because of difficulty

separating *Hydropsyche* spp. from early instars of *Cheumatopsyche etrona* Ross.

*Statistical analyses*

We compared $\log_{10}(x+1)$-transformed means of *Podostemum* biomass, abundance, and biomass for total macroinvertebrates, each FFG, and major taxa statistically among treatments at each site with repeated-measures analysis of variance using PROC MIXED (SAS for Windows, version 8, SAS Institute Inc., Cary, North Carolina). We examined significant differences ($\alpha = 0.05$) among the 3 treatments using contrast statements. We compared the mean arcsin-square root transformed proportions of individual FFGs (from the 5 and 27 August 1997 samples) among treatments using PROC GLM (SAS for Windows). We did not include shredders in FFG analyses because they composed ≤1% of mean total abundance and biomass on all dates except for one, when they composed 9.8% of total biomass. We assessed significant differences among treatments for individual FFG proportions using Tukey's method.

We used ordination to examine assemblage structure in each treatment at both sites. We did nonmetric multidimensional scaling with PC-ORD for Windows (MjM Software, Gleneden Beach, Oregon) to ordinate the $\log_{10}(x+1)$-transformed abundance and biomass for all taxa ($n = 22$ and 21, for Needmore and Iotla, respectively) that appeared on at least 2 dates for any treatment. We used the Sorensen distance measured as % dissimilarity for our analyses. We assessed significance of each axis using a Monte Carlo test, and assessed variation described by distances in the ordination space relative to the original, unreduced space by calculating a coefficient of determination (McCune and Mefford 1997).

## Results

Current velocity was similar among treatments (Table 1). Discharge declined during the study period, causing a slight reduction in velocity.

A strong positive relationship ($R^2 = 0.951$, $p = 0.001$) existed between the surface area of *P. ceratophyllum* and its biomass. Using this relationship (surface area in $mm^2$ = 46.68 + 13,580.1 × biomass in g AFDM) *P. ceratophyllum* added 3.2 to 4.2 $m^2$ (Needmore and Iotla, respectively) of surface area to each square meter of bedrock. Furthermore, when all samples from both sites were combined, there was a strong positive relationship between the $\log_{10}(x + 1)$-transformed surface area of *P. ceratophyllum* and the $\log_{10}(x + 1)$-transformed abundance ($R = 0.902$, $p < 0.001$, $n = 63$) and biomass ($R = 0.887$, $p < 0.001$, $n = 63$) of total macroinvertebrates (Fig. 1).

Podostemum *and FBOM*

At both sites, *P. ceratophyllum* standing crop in the SCRAPE treatment was lower than the CONTROL and SNIP treatments (Fig. 2). At Needmore, this difference was significant ($p \leq 0.001$), but the CONTROL and SNIP treatments were not significantly different ($p = 0.104$). Other statistical analyses comparing *Podostemum* biomass among treatments could not be completed using PROC MIXED because convergence criteria were not met or because of problems with infinite likelihood. FBOM composed <5% of total organic matter in the CONTROL and SNIP treatments (Fig. 2). FBOM biomass tended to be lowest in the SCRAPE treatment, but composed a higher proportion of total biomass (i.e., mean = 14–22%) than the other treatments. Differences in FBOM among treatments were not assessed statistically because of low standing crops (i.e., <9 g AFDM/$m^2$) relative to *Podostemum*.

*Abundance and biomass of total macroinvertebrates and FFGs*

There was a significant treatment effect on abundance and biomass of total macroinvertebrates and all FFGs at both sites (all $p < 0.001$; Fig. 3). Multiple comparisons indicated that the abundance and biomass of total macroinvertebrates and all FFGs were significantly lower in the SCRAPE treatment than in either the CONTROL or SNIP treatments. The only significant difference noted between CONTROL and SNIP treatments was for total biomass at Needmore. Significant Date and Treatment × Date interaction effects also were found at Needmore and Iotla (all $p < 0.05$), except for predator biomass.

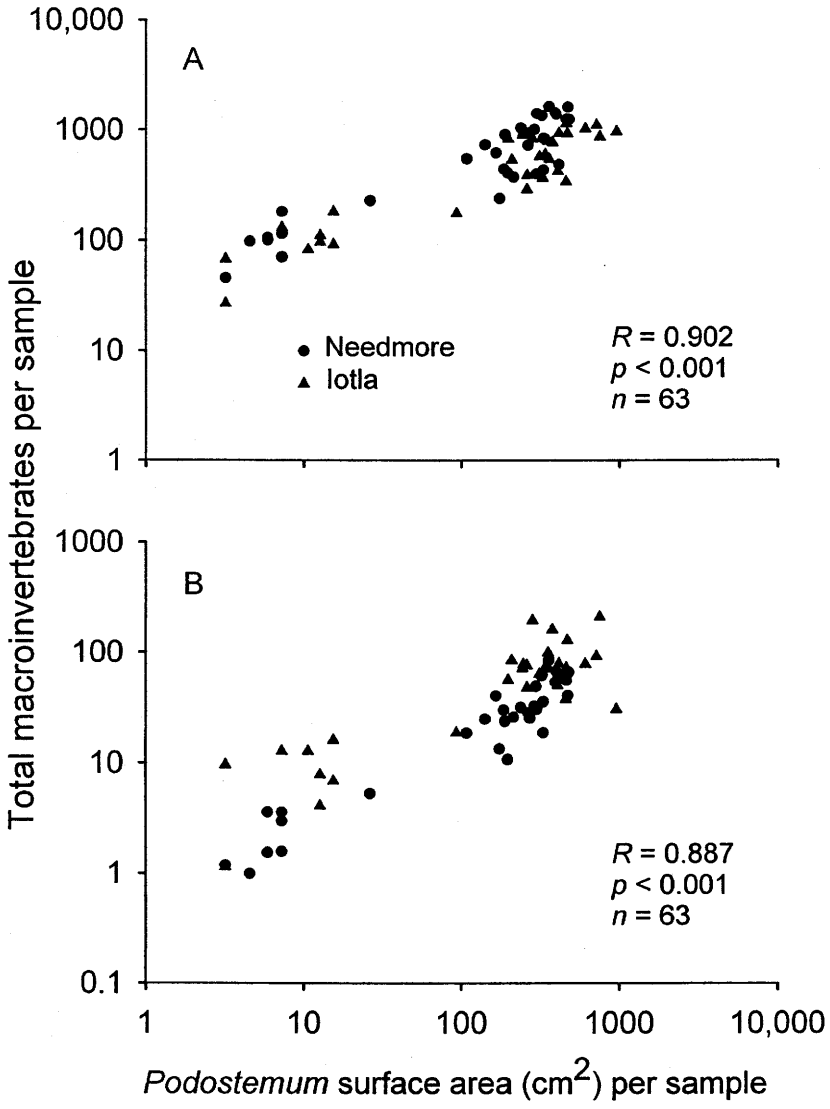


FIG. 1. Scatter plots of *Podostemum ceratophyllum* surface area in each sample versus total macroinvertebrate abundance (A) and biomass (B) in each sample.

*Proportions of each FFG*

Gatherers ($n$ = 9 taxa), scrapers ($n$ = 6 taxa), and filterers ($n$ = 5 taxa) contributed the most to total abundance at both sites (Fig. 4). Filterers, especially at Iotla, always dominated biomass. At Needmore, the proportion of gatherers was lowest in the SCRAPE treatment. The proportion of FFG abundance and biomass was generally similar among treatments.

*Individual macroinvertebrate taxa*

All of the major taxa differed significantly in abundance and biomass between the SCRAPE and the CONTROL treatments, and between the SCRAPE and SNIP treatments (Tables 2, 3). Chironomids and hydropsychids dominated (>69%) the total abundance of each treatment at Iotla (Table 4). At Needmore, the relative abundance of the top 5 individual taxa was more similar between the CONTROL and SNIP treatments compared to the SCRAPE treatment (Table 4). For example, *Baetis* and *Simulium* dominated in the SCRAPE treatment, whereas chironomids declined relative to CONTROL and SNIP. Hydropsychidae dominated biomass in the CONTROL and SNIP treatments at both sites while chironomids, *Baetis*, and hydro-

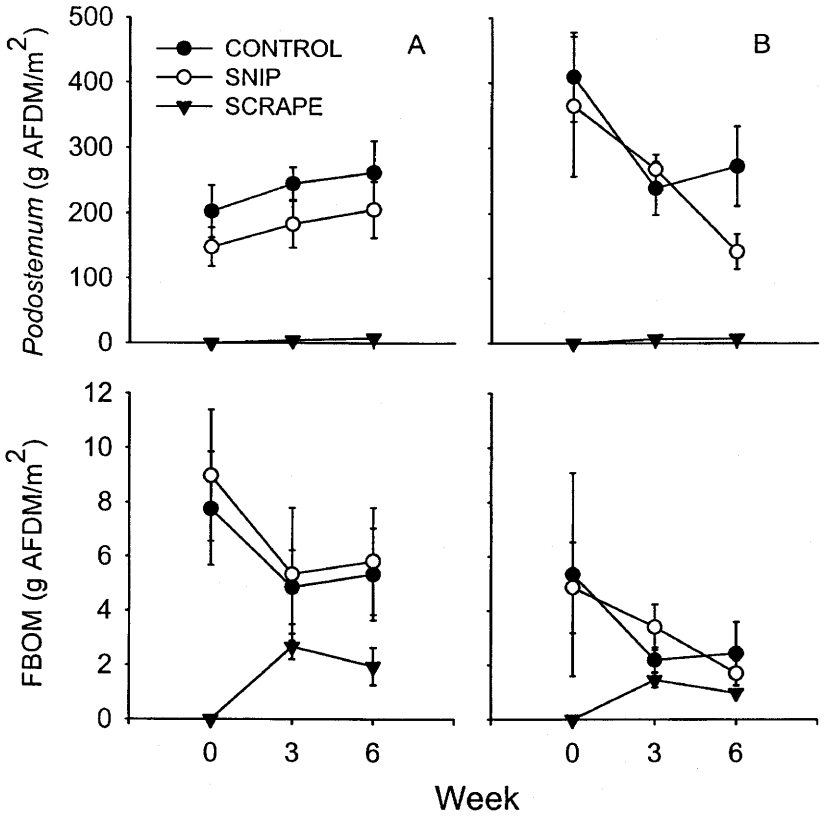


FIG. 2. Mean (±1 SE) standing crops of *Podostemum ceratophyllum* and fine benthic organic matter (FBOM) at Needmore (A) and Iotla (B).

psychids were important in the SCRAPE treatment.

*Community composition*

Community structure in the SCRAPE treatment differed from the other treatments at Needmore for both abundance and biomass (Fig. 5), primarily because of the ordination scores for *Antocha* and *Micrasema*. At Iotla, however, only the SCRAPE treatment for biomass was different from the SNIP and CONTROL treatments (Fig. 5), which was caused by scores for *Antocha*, Empididae, and *Hydroptila*. Axes 1 and 2 were significant ($p = 0.05$) for each ordination, and accounted for 82.9 to 97.5% of the total variation in abundance and biomass.

## Discussion

*Effects on total macroinvertebrate abundance and biomass*

Complete removal of *P. ceratophyllum* from bedrock habitats in the Little Tennessee River greatly reduced total macroinvertebrate abundance and biomass. Furthermore, macroinvertebrate abundance and biomass showed little recovery after 6 wk, presumably because of poor regrowth of *P. ceratophyllum* in the SCRAPE treatment. Removal of all but the basal 2 cm of *P. ceratophyllum* did not significantly reduce total macroinvertebrate abundance or biomass. Total abundance and biomass in the SNIP treatment tended to be lower than in the CONTROL treatment at both sites, but only biomass at Needmore was significantly different. These data suggest the basal portion of *P. ceratophyllum* provides important habitat and promotes benthic macroinvertebrate productivity in the Little Tennessee River. Grubaugh and Wallace (1995) and Grubaugh et al. (1996, 1997) reached similar conclusions for both the Little Tennessee River and the Oconee River, Georgia.

*Effects on macroinvertebrate functional structure*

Contrary to our prediction, we did not observe a strong shift in functional structure re-

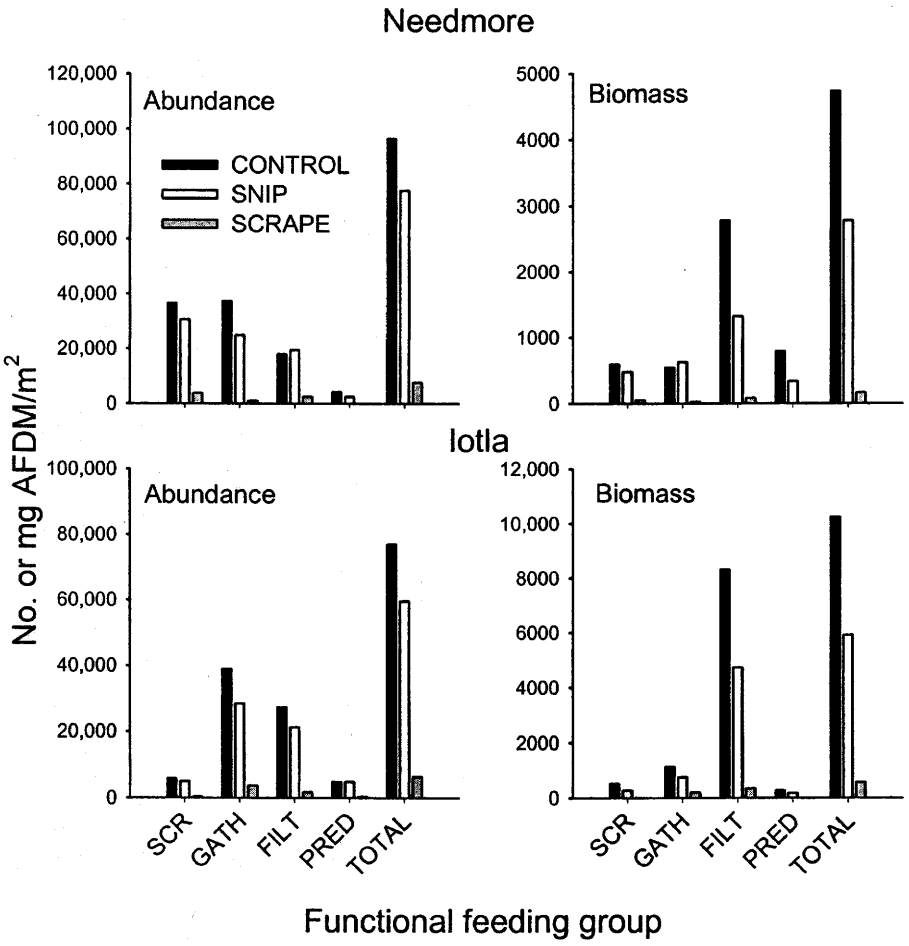


FIG. 3. Mean abundance and biomass of total macroinvertebrates and each functional feeding group across all dates at Needmore and Iotla. SCR = scrapers, SHR = shredders, GATH = collector-gatherers, FILT = collector-filterers, PRED = predators.

lated to the complete removal of *P. ceratophyllum*. We expected the proportion of filterers to decrease because of the reduction in potential attachment sites for filtering, and scrapers to increase because of the increased availability of open bedrock surface for algal growth. Although there were some signs of this functional shift, overall functional structure remained relatively similar among treatments. For example, the proportion of scraper biomass increased significantly in the SCRAPE treatment at Needmore but the proportion of filterer biomass did not change. Furthermore, there were no significant differences among treatments in the proportion of any FFG at Iotla. We offer 2 hypotheses to explain this result. First, the stems and leaves of *P. ceratophyllum* provide an extensive surface area for algal colonization. We observed large numbers of diatoms on the leaf and stem surfaces of *P. ceratophyllum*. Thus, diatoms on *P. ceratophyllum* provide a valuable food resource for scrapers, which we underestimated. Second, SCRAPE treatments were potentially colonized by macroinvertebrates inhabiting undisturbed adjacent *P. ceratophyllum*. Invertebrates could crawl or drift to the newly exposed surfaces, as seen in many studies (see reviews by Wallace 1990, Mackay 1992). Random colonization of the SCRAPE treatment by macroinvertebrates from surrounding areas would result in FFG proportions similar to the CONTROL treatment. Functional structure may have been more affected if we had removed all *Podostemum* in a reach, which would have virtually eliminated recovery by crawling during the experimental period. Large-scale disturbances affecting entire

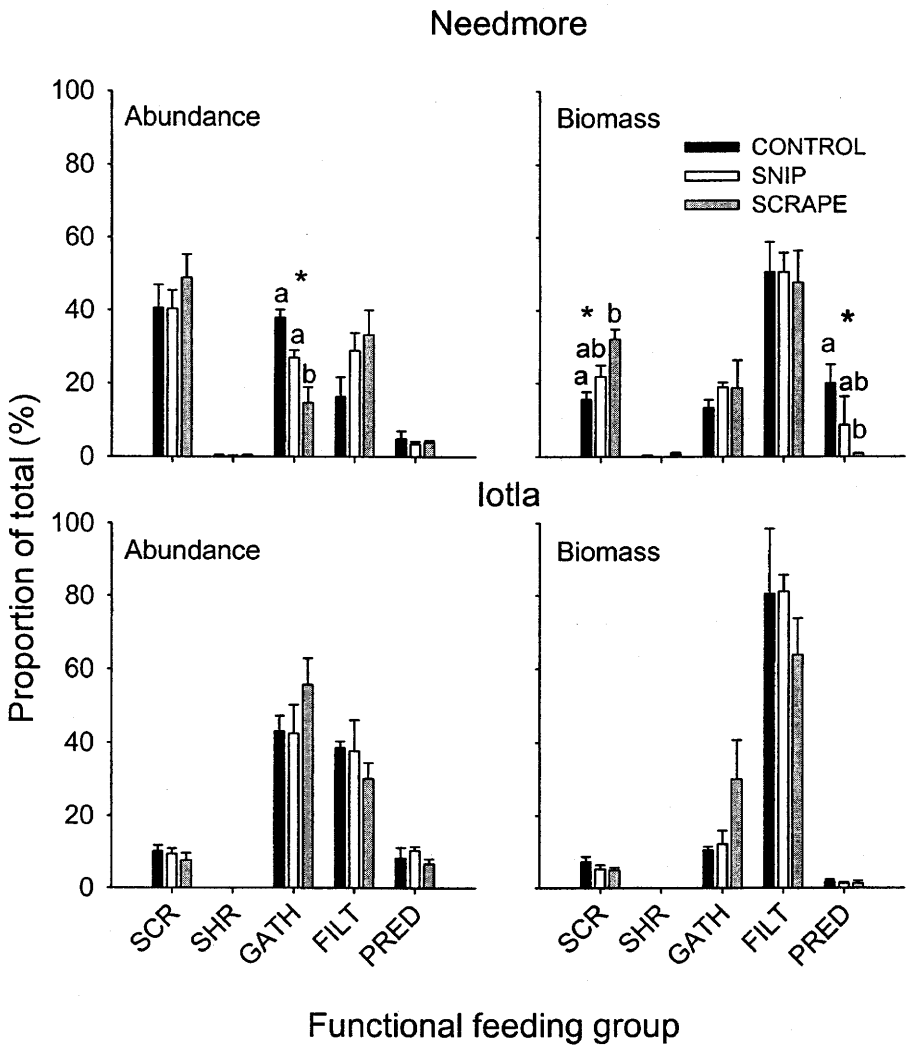


FIG. 4. Mean proportion of total abundance and biomass of each functional feeding group at Needmore and Iotla. Asterisks denote a significant treatment effect and different letters represent significant differences among individual treatments ($\alpha$ = 0.05). SCR = scrapers, SHR = shredders, GATH = collector-gatherers, FILT = collector-filterers, PRED = predators.

streams or reaches often have greater effects on the benthos because recovery can depend on distant colonists (Resh et al. 1988, Mackay 1992).

*Effects on macroinvertebrate taxa*

All of the major taxa were reduced by complete removal of *P. ceratophyllum*. Overall community composition was also different in the SCRAPE treatment compared to the CONTROL and SNIP treatments, although this difference appeared to be a result of scores for a few taxa. Few differences were noted between CONTROL and SNIP treatments for major taxa or overall community composition. As a result, the primary response of completely removing *P. ceratophyllum* was a conspicuous overall drop in abundance and biomass across most taxa, but not a major shift in community composition across all dates.

*Influence of macrophytes on aquatic macroinvertebrates*

*Podostemum* is clearly an important determinant of macroinvertebrate production in the Little Tennessee River. Macrophytes can increase macroinvertebrate populations by providing

TABLE 2. Results from repeated-measures analysis of variance for major macroinvertebrate taxa abundance and biomass at Needmore. Data were $\log_{10}(x + 1)$ transformed. For multiple comparisons, different superscript letters denote significant differences among treatment levels using contrasts. C = CONTROL, SN = SNIP, SC = SCRAPE. For other significant effects, D = significant Date effect ($p < 0.05$), T × D = significant Treatment × Date interaction effect ($p < 0.05$). Treatment and Date main effects had df = 2,9, whereas the Treatment × Date interaction effects had df = 4,9.

| Parameter | Taxon | *F*-value | *p*-value | Multiple comparison | Other significant effects |
|---|---|---|---|---|---|
| Abundance | *Baetis* spp. | 159.54 | <0.0001 | $C^aSN^aSC^b$ | D, T × D |
| | *Promoresia* sp. | 157.88 | <0.0001 | $C^aSD^aSC^b$ | D, T × D |
| | Chironomidae | 337.28 | <0.0001 | $C^aSN^aSC^b$ | D, T × D |
| | *Serratella* spp. | 31.24 | <0.0001 | $C^aSN^aSC^b$ | D |
| | Hydropsychidae | 233.34 | <0.0001 | $C^aSN^aSC^b$ | D, T × D |
| | *Simulium* spp. | 24.34 | 0.0002 | $C^aSN^aSC^b$ | D, T × D |
| Biomass | *Baetis* spp. | 232.88 | <0.0001 | $C^aSN^bSC^c$ | D, T × D |
| | *Promoresia* sp. | 137.19 | <0.0001 | $C^aSN^aSC^b$ | D |
| | Chironomidae | 85.47 | <0.0001 | $C^aSN^aSC^b$ | T × D |
| | *Serratella* spp. | 95.60 | <0.0001 | $C^aSN^aSC^b$ | D |
| | Hydropsychidae | 208.79 | <0.0001 | $C^aSN^aSC^b$ | D, T × D |
| | *Simulium* spp. | 5.44 | 0.0282 | $C^aSN^aSC^b$ | D |

habitat (= surface area), refuge from predation, substrate for epiphytic algae, and food resources (Minshall 1984, Newman 1991). There is no evidence that invertebrates consume *P. ceratophyllum* tissue in the Little Tennessee River (Rosi-Marshall and Wallace 2002). However, *P. ceratophyllum* does provide extra surface area for algal colonization, which provides additional food for scrapers.

Primarily, *P. ceratophyllum* creates habitat for benthic macroinvertebrates, especially filter feeders, through an increase in surface area available for colonization. Its highly branched growth morphology supplies 3.2 to 4.2 $m^2$ of extra surface area to bedrock habitats at Needmore and Iotla, respectively. Hence, *P. ceratophyllum* enhances bedrock habitat area for macroinvertebrates by about 3 to 4× in this river

TABLE 3. Results from repeated-measures analysis of variance for major macroinvertebrate taxa abundance and biomass at Iotla. Data were $\log_{10}(x + 1)$ transformed. Different superscript letters denote significant differences among treatment levels using contrasts. C = CONTROL, SN = SNIP, SC = SCRAPE. For other significant effects, D = significant Date effect ($p < 0.05$), T × D = significant Treatment × Date interaction effect ($p < 0.05$). Treatment and Date main effects had df = 2,9, whereas the Treatment × Date interaction effects had df = 4,9.

| Parameter | Taxon | *F*-value | *p*-value | Multiple comparison | Other significant effects |
|---|---|---|---|---|---|
| Abundance | *Baetis* spp. | 44.35 | <0.0001 | $C^aSN^aSC^b$ | D, T × D |
| | *Promoresia* sp. | 158.60 | <0.0001 | $C^aSN^aSC^b$ | D, T × D |
| | Chironomidae | 326.53 | <0.0001 | $C^aSN^bSC^c$ | D, T × D |
| | Oligochaeta | 17.38 | 0.0008 | $C^aSN^aSC^b$ | T × D |
| | Hydropsychidae | 17.00 | 0.0009 | $C^aSN^aSC^b$ | D, T × D |
| | *Isonychia* sp. | 17.66 | 0.0008 | $C^aSN^aSC^b$ | D, T × D |
| Biomass | *Baetis* spp. | 36.26 | <0.0001 | $C^aSN^aSC^b$ | T × D |
| | *Promoresia* sp. | 60.08 | <0.0001 | $C^aSN^aSC^b$ | D |
| | Chironomidae | 58.98 | <0.0001 | $C^aSN^aSC^b$ | D, T × D |
| | Oligochaeta | 24.24 | 0.0002 | $C^aSN^aSC^b$ | D, T × D |
| | Hydropsychidae | 22.85 | 0.0003 | $C^aSN^aSC^b$ | D, T × D |
| | *Isonychia* sp. | 12.06 | 0.0028 | $C^aSN^aSC^b$ | D |

TABLE 4. Proportion (%) of mean total abundance (no./m²) and biomass (mg AFDM/m²) of the dominant 10 macroinvertebrate taxa for each treatment at Iotla and Needmore.

| Abundance | | | | | |
|---|---|---|---|---|---|
| Control | | Snip | | Scrape | |
| **Iotla** | | | | | |
| Chironomidae | 44 | Chironomidae | 36 | Chironomidae | 52 |
| Hydropsychidae | 31 | Hydropsychidae | 33 | Hydropsychidae | 26 |
| Oligochaeta | 6 | Oligochaeta | 11 | *Antocha* | 5 |
| *Promoresia* | 5 | Hydracarina | 4 | Hydracarina | 4 |
| Hydracarina | 4 | *Promoresia* | 4 | *Baetis* | 4 |
| *Isonychia* | 3 | *Isonychia* | 3 | *Brachycentrus* | 2 |
| *Baetis* | 2 | Turbellaria | 3 | Oligochaeta | 1 |
| Turbellaria | 2 | *Baetis* | 2 | *Promoresia* | 1 |
| *Brachycentrus* | 1 | *Stenonema* | 2 | *Hydroptila* | 1 |
| *Hydroptila* | 1 | Tanypodinae | 1 | Empididae | 1 |
| **Total** = 77,002 | | **Total** = 59,342 | | **Total** = 9579 | |
| **Needmore** | | | | | |
| Chironomidae | 33 | Chironomidae | 28 | *Baetis* | 41 |
| *Baetis* | 21 | *Baetis* | 22 | *Simulium* | 22 |
| *Promoresia* | 17 | *Promoresia* | 17 | Chironomidae | 11 |
| Hydropsychidae | 12 | Hydropsychidae | 13 | Hydropsychidae | 10 |
| *Simulium* | 6 | *Simulium* | 12 | *Promoresia* | 9 |
| *Serratella* | 6 | *Serratella* | 4 | Hydracarina | 2 |
| Hydracarina | 2 | Hydracarina | 1 | *Serratella* | 2 |
| Turbellaria | 1 | Turbellaria | 1 | *Micrasema* | 1 |
| Tanypodinae | 1 | Tanypodinae | 1 | *Antocha* | 1 |
| *Lepidostoma* | <1 | Oligochaeta | <1 | Tanypodinae | <1 |
| **Total** 96,507 | | **Total** = 77,673 | | **Total** = 11,482 | |

depending on the time of year. This surface area estimate is conservative, however, given that it only considers standing stock biomass and not net primary productivity. Regardless, we found a strong positive relationship between surface area of *Podostemum* and total macroinvertebrate abundance and biomass. Overall, our results support previous findings that additional surface area created by aquatic plants can be a critical factor for determining invertebrate abundance in estuaries and coastal marine systems (Orth et al. 1984, Hall and Bell 1988, Fredette et al. 1990), lakes (Cyr and Downing 1988, Brown and Lodge 1993), and streams (Glime and Clemons 1972, Minshall 1984, Lee and Hershey 2000).

Some additional factors may have contributed to the strong effects observed in the SCRAPE treatment. The 6-wk duration of each experiment may have not provided enough time for significant regrowth or re-establishment of *P. ceratophyllum* and subsequent invertebrate colonization. The SCRAPE treatment resulted in the partial removal of surface biofilm as well as plant removal. The Podostemaceae require a surface biofilm for attachment in very rapidly flowing areas (Jager-Zurn and Grubert 2000). They attach to thread-like substances found in cyanobacteria and extracellular polymeric substances in biofilms using adhesive hairs. Development of a thick, physically complex, surface biofilm on inorganic substrates can occur in ~3 wk and depends on current velocity (Battin et al. 2003). Thus, the partial removal of biofilm, coupled with its importance as an attachment matrix, could have contributed to the slow re-establishment of *Podostemum*.

The ability of *P. ceratophyllum* to facilitate high macroinvertebrate productivity is similar to the ecological roles played by bryophytes and the filamentous alga *Cladophora*. Thick growth of mosses provides a substantial 3-dimensional habitat atop hard surfaces for macroinvertebrates (e.g., Glime and Clemons 1972, Suren 1991, Stream Bryophyte Group 1999). Similarly, *Cladophora* mats support a dense macroinverte-

TABLE 4. Extended.

| Biomass | | | | | |
|---|---|---|---|---|---|
| Control | | Snip | | Scrape | |
| Hydropsychidae | 60 | Hydropsychidae | 63 | Hydropsychidae | 55 |
| *Isonychia* | 15 | *Isonychia* | 15 | Chironomidae | 34 |
| Chironomidae | 10 | Chironomidae | 11 | *Brachycentrus* | 5 |
| *Brachycentrus* | 7 | *Promoresia* | 3 | *Hydroptila* | 3 |
| *Promoresia* | 4 | *Brachycentrus* | 3 | *Promoresia* | 1 |
| *Perlesta* | 2 | *Perlesta* | 2 | *Antocha* | 1 |
| *Serratella* | 1 | Turbellaria | 1 | Empididae | 1 |
| *Baetis* | 1 | *Serratella* | 1 | *Baetis* | 1 |
| *Hydroptila* | 1 | *Baetis* | 1 | Turbellaria | <1 |
| Turbellaria | <1 | Oligochaeta | <1 | Hydracarina | <1 |
| **Total** = 10,254 | | **Total** = 5964 | | **Total** = 862 | |
| Hydropsychidae | 55 | Hydropsychidae | 43 | Hydropsychidae | 31 |
| *Paragnetina* | 9 | *Serratella* | 14 | *Baetis* | 29 |
| *Baetis* | 7 | *Baetis* | 9 | *Simulium* | 19 |
| *Serratella* | 6 | *Promoresia* | 9 | Chironomidae | 9 |
| *Promoresia* | 6 | *Paragnetina* | 7 | *Serratella* | 7 |
| Chironomidae | 5 | Chironomidae | 6 | *Promoresia* | 3 |
| *Corydalus* | 4 | *Simulium* | 5 | *Micrasema* | 2 |
| *Perlesta* | 2 | *Perlesta* | 4 | *Antocha* | <1 |
| *Simulium* | 2 | *Drunella* | 2 | Hydracarina | <1 |
| *Brachycentrus* | 1 | Turbellaria | <1 | Perlodidae | <1 |
| **Total** = 4730 | | **Total** = 2778 | | **Total** = 252 | |

brate community (Dodds and Gudder 1992, Creed 1994). Bryophytes and *Cladophora* also serve as a substrate for epiphytic algae, which can serve as food for grazing invertebrates (Dodds 1991, Dodds and Gudder 1992, Suren and Winterbourn 1992). FBOM trapped in these mats also provides food for gatherers (Glime and Clemons 1972, Dodds 1991, Suren and Winterbourn 1992). Although the standing crops of FBOM were low in our experiment, this material likely turns over rapidly and serves as a food resource in *Podostemum* mats. Clearly, the ecological role of *Podostemum*, bryophytes, and *Cladophora* in streams is much greater than their productivity alone.

Kaenel et al. (1998) found pronounced short-term negative effects on total macroinvertebrate abundance in 2 Swiss lowland streams after experimental reductions of plant biomass. Taxa that depended on macrophytes for habitat (i.e., Simuliidae, Chironomidae, and Hydracarina) were especially sensitive to plant removal, whereas highly mobile taxa (i.e., *Baetis*) and sediment-dwelling taxa (i.e., Trichoptera, Bivalvia, and Nematoda) were insensitive. Our study found pronounced effects on all major taxa regardless of mobility, perhaps because our scraping treatment (100% biomass removal) was more severe than the manual cutting of plants (84–87% biomass removal) in Kaenel et al. (1998). The *Podostemum* examined in our study grew on bedrock outcrops, which allowed for their complete removal, unlike the *Ranunculus fluitans* Lam. and *Myriophyllum spicatum* L. removed from sand and fine-gravel habitats in the Swiss streams. Thus, sediment-dwelling taxa were not entirely eliminated by the macrophyte treatment in Kaenel et al. (1998). Kaenel et al. (1998) also found that the abundance of macroinvertebrates recovered within 4 to 6 mo. We do not know the length of time needed for recovery of macroinvertebrate abundance and biomass in the Little Tennessee River, but suspect it depends on the recovery of *P. ceratophyllum*.

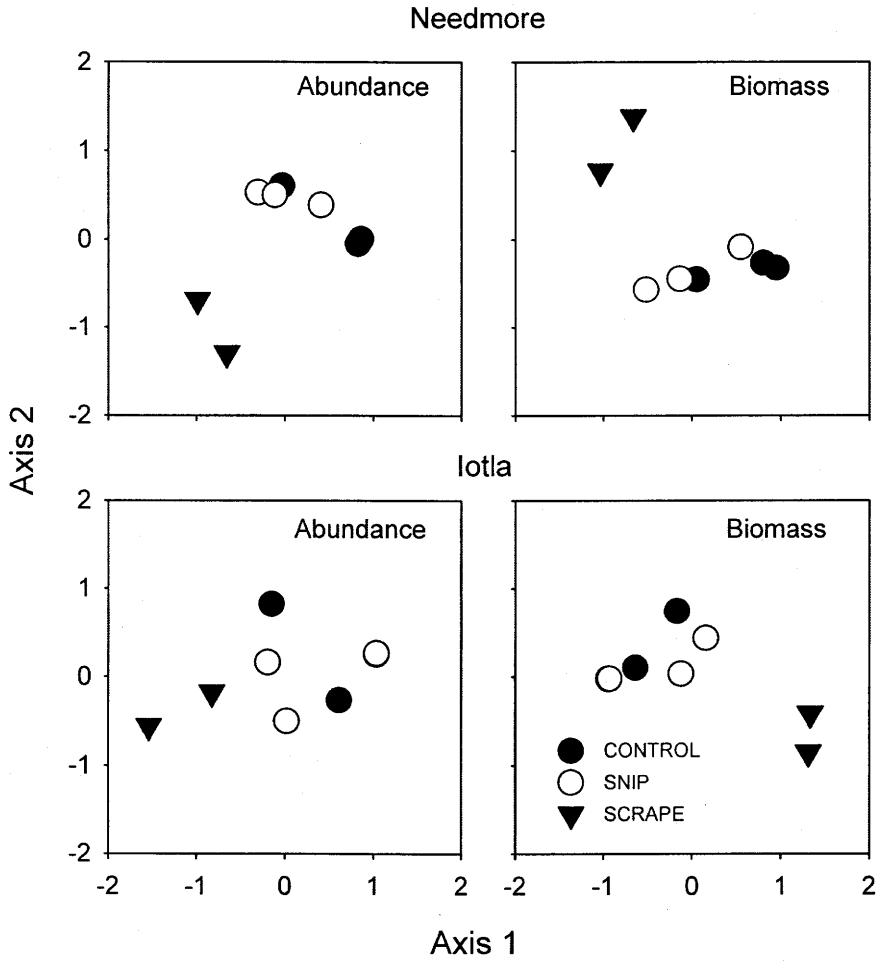


FIG. 5. Ordination plots of the first 2 axes from nonmetric multidimensional scaling analyses of each treatment based on the abundance and biomass of taxa that appeared on at least 2 dates for any treatment at Needmore and Iotla.

*Role of Podostemaceae in stream ecosystems*

The Podostemaceae are distributed widely and play a variety of important roles in streams worldwide. Wuillot (1994) found very high species richness and density of Baetidae in the erect stems of Podostemaceae in the River Niandan, Guinea. In 3rd- and 4th-order streams of Costa Rica, dense mats of *Marathrum* (Podostemaceae) supported extremely high densities of caddisflies and predatory *Corydalus*, and provided oviposition sites for odonates (de la Rosa 1995). One species of caddisfly, *Brachycentrus etowahensis* Wallace, is restricted to *P. ceratophyllum*-covered habitats in the southeastern US (Wallace 1971, Willats 1998). *Podostemum* mats served as a source habitat (sensu Pulliam 1988) for the pleurocerid snail, *Oxytrema suturalis* Haldeman, in the Yellow River, Georgia (Krieger and Burbanck 1976). In addition to habitat for invertebrates, presence of *P. ceratophyllum* occasionally is associated with certain fish species such as the riverweed darter *Etheostoma podostemone* Jordan (Jenkins and Burkhead 1994, Connelly et al. 1999). The high densities of stream invertebrates in *P. ceratophyllum* mats probably serve as a valuable prey resource for benthos-feeding fish. For example, we frequently observed redhorse suckers foraging in the *P. ceratophyllum* beds while we were sampling. An additional ecological value of *P. ceratophyllum* is its importance in detritus dynamics because it breaks down rapidly (Hill and Webster 1982) and can contribute a seasonally important pulse of organic matter to the detrital food web in mid-sized rivers (Hill and

Webster 1983). Finally, *P. ceratophyllum* may be a useful indicator species of high water quality because of its intolerance of siltation and need for high concentrations of dissolved oxygen (Meijer 1976, Philbrick and Crow 1983, Philbrick and Novelo 1995). Our experiment provides additional evidence for the valuable role of *P. ceratophyllum* in stream ecosystems.

## Acknowledgements

Sue Eggert and Alonso Ramirez assisted in field collections, and Peter Esselman and Mary Palmer assisted in the laboratory. Karen Blocksom provided statistical guidance. Wyatt Cross, Alonso Ramirez, Chris Pennuto, David Rosenberg, and 2 anonymous reviewers provided helpful comments on an early draft. The National Science Foundation (DEB-9632854 and DEB-0218001) supported this work through the Coweeta LTER program. JJH also acknowledges support by the mini-grant program and the Department of Biology, Coastal Carolina University.

## Literature Cited

ALLAN, J. D. 1995. Stream ecology: structure and function of running waters. Chapman and Hall, London, UK.

BATTIN, T. J., L. A. KAPLAN, J. D. NEWBOLD, X. CHENG, AND C. HANSEN. 2003. Effects of current velocity on the nascent architecture of stream microbial biofilms. Applied and Environmental Microbiology 69:5443–5452.

BENKE, A. C., A. D. HURYN, L. A. SMOCK, AND J. B. WALLACE. 1999. Length–mass relationships for freshwater macroinvertebrates in North America, with particular reference to the southeastern United States. Journal of the North American Benthological Society 18:308–343.

BROWN, K. M., AND D. M. LODGE. 1993. Gastropod abundance in vegetated habitats: the importance of specifying null models. Limnology and Oceanography 38:217–225.

CATTANEO, A., AND J. KALFF. 1980. The relative contribution of aquatic macrophytes and their epiphytes to the production of macrophyte beds. Limnology and Oceanography 25:280–289.

CONNELLY, W. J., D. J. ORTH, AND R. K. SMITH. 1999. Habitat of the riverweed darter, *Etheostoma podostemone* Jordan, and the decline of riverweed, *Podostemum ceratophyllum*, in the tributaries of the Roanoke River, Virginia. Journal of Freshwater Ecology 14:93–102.

CREED, R. P. 1994. Direct and indirect effects of crayfish grazing in a stream community. Ecology 75: 2091–2103.

CYR, H., AND J. A. DOWNING. 1988. Empirical relationships of phytomacrofaunal abundance to plant biomass and macrophyte bed characteristics. Canadian Journal of Fisheries and Aquatic Sciences 45:976–984.

DE LA ROSA, C. 1995. Middle American streams and rivers. Pages 189–218 in C. E. Cushing, K. W. Cummins, and G. W. Minshall (editors). Ecosystems of the world: river and stream ecosystems. Elsevier, Amsterdam, The Netherlands.

DODDS, W. K. 1991. Community interactions between the filamentous alga *Cladophora glomerata* (L.) Kuetzing, its epiphytes, and epiphyte grazers. Oecologia (Berlin) 85:572–580.

DODDS, W. K., AND B. J. F. BIGGS. 2002. Water velocity attenuation by stream periphyton and macrophytes in relation to growth form and architecture. Journal of the North American Benthological Society 21:2–15.

DODDS, W. K., AND D. A. GUDDER. 1992. The ecology of *Cladophora*. Journal of Phycology 28:415–427.

ENGLISH, W. R. 1987. Three inexpensive aquatic samplers for the benthos, drift and emergent fauna. Entomological News 98:171–179.

EVERITT, D. T., AND J. M. BURKHOLDER. 1991. Seasonal dynamics of macrophyte communities from a stream flowing over granite flatrock in North Carolina, USA. Hydrobiologia 222:159–172.

FREDETTE, T. J, R. J. DIAZ, J. VAN MONTFRANS, AND R. J. ORTH. 1990. Secondary production within a seagrass bed (*Zostera marina* and *Ruppia maritima*) in Lower Chesapeake Bay. Estuaries 13:431–440.

FRITZ, K. M., AND J. W. FEMINELLA. 2003. Substratum stability associated with the riverine macrophyte *Justicia americana*. Freshwater Biology 48:1630–1639.

GLIME, J. M., AND R. M. CLEMONS. 1972. Species diversity of stream insects on *Fontinalis* spp. compared to diversity on artificial substrates. Ecology 53:458–464.

GREGG, W. W., AND F. L. ROSE. 1982. The effects of aquatic macrophytes on the stream microenvironment. Aquatic Botany 14:309–324.

GRUBAUGH, J. W., AND J. B. WALLACE. 1995. Functional structure and production of the benthic community in a Piedmont river: 1956–1957 and 1991–1992. Limnology and Oceanography 40:490–501.

GRUBAUGH, J. W., J. B. WALLACE, AND E. S. HOUSTON. 1996. Longitudinal changes of macroinvertebrate communities along an Appalachian stream continuum. Canadian Journal of Fisheries and Aquatic Sciences 53:896–909.

GRUBAUGH, J. W., J. B. WALLACE, AND E. S. HOUSTON. 1997. Production of benthic macroinvertebrate

communities along a southern Appalachian river continuum. Freshwater Biology 37:581–596.

HALL, M. O., AND S. S. BELL. 1988. Response of small motile epifauna to complexity of epiphytic algae on seagrass blades. Journal of Marine Research 46:613–630.

HILL, B. H., AND J. R. WEBSTER. 1982. Aquatic macrophyte breakdown in an Appalachian river. Hydrobiologia 89:53–59.

HILL, B. H., AND J. R. WEBSTER. 1983. Aquatic macrophyte contribution to the New River organic matter budget. Pages 273–282 in T. D. Fontaine and S. M. Bartell (editors). Dynamics of lotic ecosystems. Ann Arbor Science Publishers, Ann Arbor, Michigan.

HURYN, A. D., AND J. B. WALLACE. 2000. Life history and production of stream insects. Annual Review of Entomology 45:83–110.

HYNES, H. B. N. 1970. The ecology of running waters. Liverpool University Press, Liverpool, UK.

JACOBSEN, D., AND K. SAND-JENSEN. 1992. Herbivory of invertebrates on submerged macrophytes from Danish freshwaters. Freshwater Biology 28:301–308.

JAGER-ZURN, I., AND M. GRUBERT. 2000. Podostemaceae depend on sticky biofilms with respect to attachment to rocks in waterfalls. International Journal of Plant Sciences 161:599–607.

JENKINS, R. E., AND N. M. BURKHEAD. 1994. Freshwater fishes of Virginia. American Fisheries Society, Bethesda, Maryland.

KAENEL, B. R., C. D. MATTHAEI, AND U. UEHLINGER. 1998. Disturbance by aquatic plant management in streams: effects on benthic invertebrates. Regulated Rivers: Research and Management 14:341–356.

KRIEGER, K. A., AND W. D. BURBANCK. 1976. Distribution and dispersal mechanisms of Oxytrema (= Goniobasis) suturalis Haldeman (Gastropoda: Pleuroceridae) in the Yellow River, Georgia, U.S.A. American Midland Naturalist 95:49–63.

LEE, J. O., AND A. E. HERSHEY. 2000. Effects of aquatic bryophytes and long-term fertilization on arctic stream insects. Journal of the North American Benthological Society 19:697–708.

LODGE, D. M. 1991. Herbivory on freshwater macrophytes. Aquatic Botany 41:195–224.

MACKAY, R. 1992. Colonization by lotic macroinvertebrates: a review of processes and patterns. Canadian Journal of Fisheries and Aquatic Sciences 49:617–628.

MADSEN, J. D., P. A. CHAMBERS, W. F. JAMES, E. W. KOCH, AND D. F. WESTLAKE. 2001. The interaction between water movement, sediment dynamics and submersed macrophytes. Hydrobiologia 444: 71–84.

MASON, W. T., AND P. P. YEVICH. 1967. The use of phloxine B and rose bengal stains to facilitate sorting benthic samples. Transactions of the American Microscopical Society 86:221–223.

MCCUNE, B., AND M. J. MEFFORD. 1997. Multivariate analysis of ecological data, version 3.20. MjM Software, Gleneden Beach, Oregon.

MEIJER, W. 1976. A note on *Podostemum ceratophyllum* Michx., as an indicator of clean streams in and around the Appalachian Mountains. Castanea 41: 319–324.

MERRITT, R. W., AND K. W. CUMMINS (EDITORS). 1996. An introduction to the aquatic insects of North America. 3rd edition. Kendall/Hunt Publishing, Dubuque, Iowa.

MINSHALL, G. W. 1984. Aquatic insect-substratum relationships. Pages 358–400 in V. H. Resh and D. M. Rosenberg (editors). The ecology of aquatic insects. Praeger Publishers, New York.

MINSHALL, G. W., J. T. BROCK, AND T. W. LAPOINT. 1982. Characterization and dynamics of benthic organic matter and invertebrate functional feeding group relationships in the Upper Salmon River, Idaho (U.S.A.). Internationale Revue der gesamten Hydrobiolgie 67:793–820.

NELSON, D. J., AND D. C. SCOTT. 1962. Role of detritus in the productivity of a rock-outcrop community in a Piedmont stream. Limnology and Oceanography 7:396–413.

NEWMAN, R. M. 1991. Herbivory and detritivory on freshwater macrophytes by invertebrates: a review. Journal of the North American Benthological Society 10:89–114.

ORTH, R. J., K. L. HECK, AND J. VAN MONTFRANS. 1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. Estuaries 7:339–350.

PARKER, C. R., AND J. R. VOSHELL. 1983. Production of filter-feeding Trichoptera in an impounded and free-flowing river. Canadian Journal of Zoology 61:70–87.

PERCIVAL, E. AND H. WHITEHEAD. 1929. A quantitative study of the fauna of some types of stream-bed. Journal of Ecology 17:282–314.

PHILBRICK, C. T., AND G. E. CROW. 1983. Distribution of *Podostemum ceratophyllum* Michx. (Podostemaceae). Rhodora 85:325–334.

PHILBRICK, C. T., AND A. NOVELO. 1995. New world Podostemaceae—ecological and evolutionary enigmas. Brittonia 47:210–222.

PULLIAM, H. R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652–661.

RESH, V. H., A. V. BROWN, A. P. COVICH, M. E. GURTZ, H. W. LI, G. W. MINSHALL, S. R. REICE, A. L. SHELDON, J. B. WALLACE, AND R. WISSMAR. 1988. The role of disturbance in stream ecology. Journal of the North American Benthological Society 7:433–455.

ROSI-MARSHALL, E. J., AND J. B. WALLACE. 2002. In-

vertebrate food webs along a stream resource gradient. Freshwater Biology 47:129–141.

SAND-JENSEN, K. 1998. Influence of submerged macrophytes on sediment composition and near-bed flow in lowland streams. Freshwater Biology 39: 663–679.

STREAM BRYOPHYTE GROUP. 1999. Roles of bryophytes in stream ecosystems. Journal of the North American Benthological Society 18:151–184.

SUREN, A. M. 1991. Bryophytes as invertebrate habitat in two New Zealand alpine streams. Freshwater Biology 26:399–418.

SUREN, A. M., AND M. J. WINTERBOURN. 1992. The influence of periphyton, detritus and shelter on invertebrate colonization of aquatic bryophytes. Freshwater Biology 27:327–339.

SWANK, W. T., AND P. V. BOLSTAD. 1994. Cumulative effects of land use practices on water quality. Pages 409–422 in N. E. Peters, R. J. Allan, and V. V. Tsirkunov (editors). Hydrological, chemical, and biological processes of transformation and transport of contaminants in aquatic environments. International Association of Hydrological Sciences Publication 219. IAHS Press, Wallingford, Oxfordshire, UK.

WALLACE, J. B. 1971. A new species of *Brachycentrus* from Georgia with two unusual larval characters (Trichoptera: Brachycentridae). Entomological News 82:313–321.

WALLACE, J. B. 1990. Recovery of lotic macroinvertebrate communities from disturbance. Environmental Management 14:605–620.

WATERS, T. F. 1969. Subsampler for dividing large samples of stream invertebrate drift. Limnology and Oceanography 14:813–815.

WILLATS, A. J. B. 1998. Production, diet and microhabitat use of *Brachycentrus etowahensis* Wallace (Trichoptera: Brachycentridae). MS Thesis, University of Georgia, Athens, Georgia.

WILM, H. G., AND H. C. STOREY. 1944. Velocity-head rod calibrated for measuring stream flow. Civil Engineering 14:475–476.

WUILLOT, J. 1994. Microdistribution of larval Baetidae in the dry season on the rocky substrates of River Niandan (Guinea). Archiv für Hydrobiologie 131: 465–476.

*Received: 28 June 2003*
*Accepted: 10 August 2004*