Hydrobiologia **519:** 29–37, 2004.
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Quality of suspended fine particulate matter in the Little Tennessee River

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Received 28 January 2003; in revised form 6 November 2003; accepted 11 November 2003

Key words: food quality, seston, chironomids, instantaneous growth

Abstract

Fine particulate organic matter is a major food resource in southeastern river food webs, but natural variability in the quality of this resource has not been assessed. We measured the quality of suspended fine particulate matter (SFPM) along the Little Tennessee River at four sites ranging from 5th to 7th order. SFPM quality was measured using traditional measures: nitrogen to carbon ratio (N/C), calories (cal g^{-1} DM), % lipids, % inorganic matter, bacteria (# cells g^{-1} DM) and % diatoms. Instantaneous growth rates of chironomids fed SFPM were used as an integrated measure of food quality. Traditional measures of SFPM quality varied among sites, with higher N/C and % inorganic downstream, higher % lipids and bacteria upstream, and no pattern in the % diatoms and calories. Although percent mortality did not differ among chironomids fed SFPM from different sites, instantaneous growth rates (IGRs) of chironomids fed SFPM from the most downstream site were significantly higher than those fed SFPM from the most upstream site, implying higher food quality at the downstream site. IGRs were not significantly different among seasons for any site. The traditional measures individually and in combination (using principal components analysis) were not related to IGRs. IGRs are a more realistic indicator of food quality than measures of individual attributes, because IGRs integrate the consumer's response. The quality of a food resource is not merely the sum of its measurable parts (% lipids, calories, % inorganic, and diatoms), and one or a combination of measures is not adequate to predict food quality. The Little Tennessee River has very high secondary production of filtering invertebrates at the 7th order site. The quality of SFPM as a food resource and extensive favorable habitat of macrophytes on bedrock, support the high secondary production of filtering invertebrates at this site.

Introduction

Fine particulate organic matter (FPOM) is a major food resource in stream food webs (Wallace et al., 1987; Couch et al., 1996; Benke & Wallace, 1997; Hall & Meyer, 1998; Rosi-Marshall & Wallace, 2002) and is the dominant basal resource in large southeastern river food webs (Benke & Wallace, 1997; Rosi-Marshall & Wallace, 2002). It is consumed by aquatic invertebrates, which support fish and other higher trophic levels; therefore FPOM supports many economically, recreationally, and ecologically important species. Few studies have examined natural variability in FPOM quality (Meyer et al., 2000; Vos et al., 2000) despite its demonstrated importance in large river food webs.

FPOM quality likely reflects the nature of its formation and the types of organic matter from which it is derived. It can be formed by the breakdown of larger particles (leaves, animals, etc.) or the flocculation of dissolved organic matter (DOM). As water passes over land or through the soil, it picks up dissolved and colloidal materials, and instream organic matter decomposes or actively contributes to the pool of DOM (leaf leaching, algal exudates, bacterial exopolymers, etc.). Both chemical (Warren & Zimmerman, 1993) and physical processes (Lush & Hynes, 1973; Alber & Valiela, 1994; Wotton, 1996) cause DOM to aggregate into particles which are a substrate for bacterial colonization (Alber & Valiela, 1994; Wotton, 1996). Chemical and physical breakdown of large particles, such as leaves and algae, also contribute to the pool of FPOM. All of these processes interact to form the mixed resource called FPOM.

FPOM quality likely varies among sites as a function of organic matter sources, because it is a mixture of larger particles, DOM quality and amount of inorganic particles present. Anderson & Cummins (1979) predicted a nutritional food gradient with food quality increasing from wood, terrestrial leaf litter, fine particulate matter, decomposing vascular hydrophytes and filamentous algae, live algae, to animal tissue (Fuller & Mackay, 1981; Pandian & Marian, 1986; Fuller et al., 1988; Rosillon, 1988; Fuller & Desmond, 1997). Fewer studies examine the natural variability in quality of fine particulate matter as a food resource (Meyer et al., 2000), even though FPOM is a mixture of numerous food resource types (bacteria, algae, leaf particles, etc.). There has been research on the quality of FPOM's constituent parts (Fuller et al., 1988; Vos et al., 2000); however, measurement of natural FPOM variability necessitates examination of the resource as a whole.

In order to obtain naturally varying FPOM, particles were collected during different seasons along the Little Tennessee River. FPOM in streams can be found in the benthos and suspended in the water column. Fine particulate organic matter ranges in size from 0.45 μm to 1 mm (Wallace & Grubaugh, 1996); particles were collected that encompass a large portion of this range. Suspended FPOM was collected during base flow which represents a portion of what is available to filter-feeders and collector-gatherers. We use the term suspended fine particulate matter (SFPM) for this material because natural suspended FPOM also contains inorganic particles. Our objective was to determine if there is a change in the quality of SFPM with season and catchment area. The River Continuum Concept (RCC) predicts that labile forms of dissolved compounds and fine particles are used or absorbed upstream and that downstream areas will contain more refractory compounds (Vannote et al., 1980). This would result in lower quality SFPM at downstream sites. The secondary production of filtering insects which consume SFPM increases downstream (Grubaugh et al., 1997), which suggests that the quality of SFPM may increase downstream. As a river widens, the potential for autochthonous production increases and the importance of allochthonous inputs can decline (Vannote et al., 1980; Rosi-Marshall & Wallace, 2002). According to the nutritional food gradient (Anderson & Cummins, 1979), when higher autochthonous resources contribute to SFPM, its quality may be higher. In mid-order streams, autochthonous and allochthonous resources are likely to vary in importance throughout the year with changing riparian cover and light availability. We hypothesized that the quality of SFPM would be higher at the more downstream sites and that the seasonal variability of SFPM quality would increase in the mid-orders. To test these hypotheses, the quality of SFPM collected at four sites during four seasons was measured using traditional measures of food quality (nitrogen to carbon ratio, % diatoms, % inorganic, caloric content, % lipids and bacterial abundance). Instantaneous growth rates of chironomids fed SFPM was used as an integrative measure of food quality.

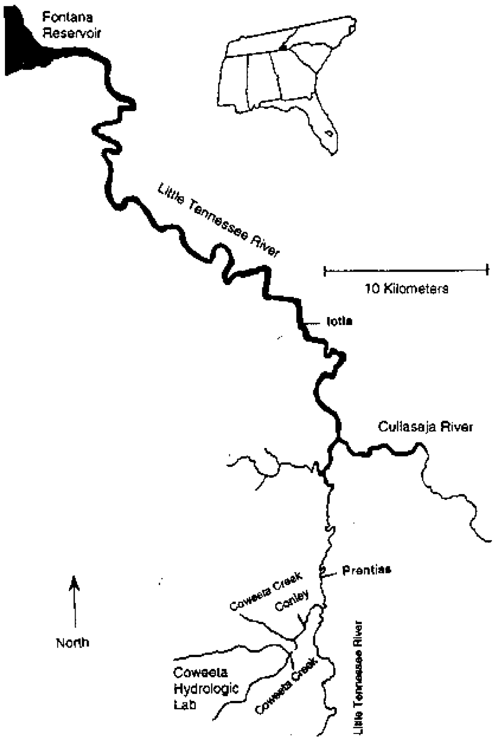

Figure 1. Map of study sites along the Little Tennessee River, North Carolina, USA (modified from Grubaugh, 1995).

Description of sites studied

Suspended fine particulate matter (SFPM) was collected from four sites (Table 1) in the Little Tennessee River drainage (LTR), Macon county, North Caro-

Table 1. Study site characteristics along the Coweeta Creek – Little Tennessee River, Macon Co. North Carolina (modified from Grubaugh et al., 1996, *Rosi, 1997 and †Grubaugh et al., 1997).

Coweeta Creek	Conley Road	Prentiss	Iotla	
Stream system	Coweeta Creek	Coweeta Creek	Little Tennessee River	Little Tennessee River
Stream order	5	5	6	7
Catchment area (ha)	1548	4163	36 260	83 660
Elevation (m above sea level)	671	633	620	597
Mean annual discharge ($m^3 \cdot s^{-1}$)	0.58	1.35	10.85	22.18
Mean width (m)	7.2	15	25	60
Mean depth (cm)	25	25	50	50
Annual degree days	4078	4389	4763	4922
Podostemum ceratophylum covered cobbles	0	62%	14%	27%
P. ceratophylum covered bedrock	0	0	0	38%
POM concentration (g AFDM l^{-1})*	0.002	0.001	0.003	0.004
Habitat weighted collector/filterer secondary production ($gm^{-2}yr^{-1}$)†	1.1	9.9	13.8	122.8

lina (35° 03′ N and 83° 25′ W) (Fig. 1). The LTR is in the Blue Ridge province and flows north from Georgia into North Carolina before entering Fontana Reservoir. The LTR drains an area of crystalline rock which results in low streamwater ion concentrations (Swank & Bolstad, 1994). The secondary production and trophic basis of production of the macroinvertebrate assemblage were previously measured at the four sites (Grubaugh et al., 1997, Rosi-Marshall & Wallace, 2002). These sites range from mid to high (5–7) stream order. SFPM is an important food resource at these sites, and its importance increases at the larger sites (Rosi-Marshall & Wallace, 2002).

The first two sites, Coweeta Creek and Conley (5th order), drain predominantly forested basins (over 90%) (Swank & Bolstad, 1994). Coweeta Creek has the greatest canopy closure because of a riparian evergreen shrub (*Rhododendron maxima*, L.), that reduces light and potential primary production throughout the year. Conley, downstream of Coweeta Creek, has a deciduous canopy cover, which may increase the seasonality of primary production. The two lower sites, Prentiss (sixth order) and Iotla (seventh order) are on the LTR mainstem with forested riparian zones that provide little stream shading because of large stream width.

Methods

Collection and measurement of suspended fine particles

SFPM (from 20 μm to 1mm) was collected from the four sites described above in January, May, July and October 1998. Mean monthly stream flow for the months sampled was 23.4, 14.7, 5.0, and 4.2 m^3 s^{-1} for January, May, July and October, respectively (HUC Code 06010202, http://waterdata.usgs.gov/nwis/monthly, 19 April, 2002). Samples were collected during an extended period of base flow in each season. A 20 μm net with a 1 mm sieve attached to the opening was used to collect particles. The net was placed in the flow of the channel from 10–20 min to collect an integrated sample of SFPM, which was placed on ice and brought back to the lab for analysis. The following chemical attributes of SFPM for each site and season were measured: lipid content, nitrogen to carbon ratios, % inorganic, and calories. The proportion of leaf material, diatoms, and amorphous detritus was also measured. Four subsamples were used to measure N/C, % inorganic, % diatoms, % leaves, and % amorphous detritus. One subsample was analyzed for % lipids and calories. A subsample of the SFPM was frozen for later use in the growth experiment, and bacterial abundance was measured on four subsamples at the conclusion of the growth experiment.

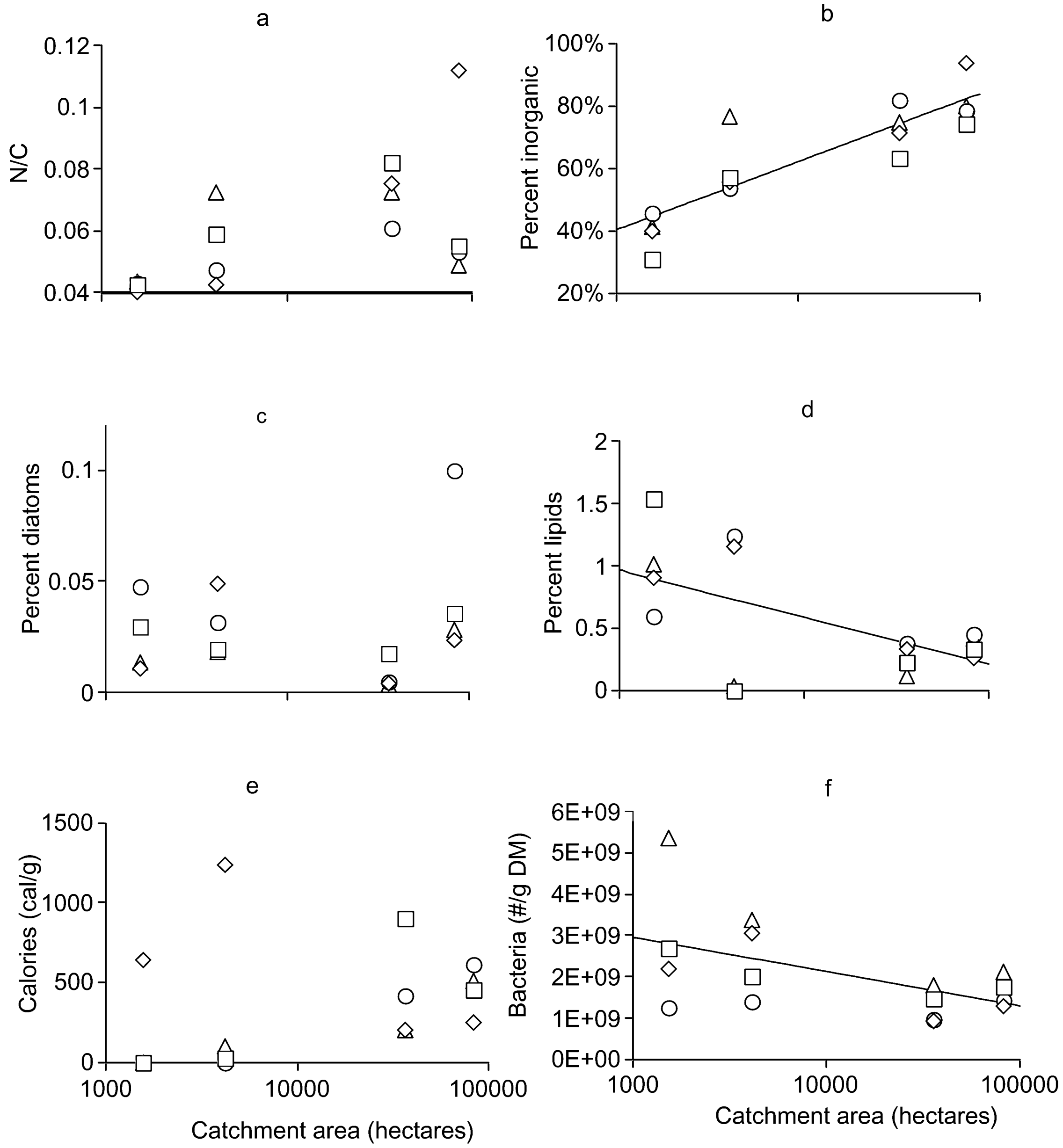

Figure 2. Relationship between catchment area (CA in ha) and quality of SFPM collected during each season [January (◊), May (○), July (△) and October (□), 1998]. SFPM quality is measured in terms of: (a) N/C ($r^2 = 0.20$, $p = 0.09$), (b) % inorganic ($r^2 = 0.76$, $p = 0.001$, $y = -0.25 + 0.09 \log \text{CA}$), (c) % diatoms ($r^2 = 0.09$, $p = 0.25$), (d) % lipids ($r^2 = 0.45$, $p = 0.005$, $y = 2.3 - -0.18 \log \text{CA}$), (e) calories (cal g $^{-1}$ DM) ($r^2 = 0.002$, $p = 0.88$), (f) bacteria (cells g^{-1} DM) ($r^2 = 0.28$, $p = 0.03$, $y = 5.45 - -3.6x10^8 \log \text{CA}$).

Lipid content was measured using an ether extraction technique (APHA, 1985) and is expressed as % lipids (100 * mg lipids mgDM^{-1}). Calories (cal g^{-1} DM) were measured using a bomb-calorimeter. N/C ratio (by mass) was measured using a Carlo Erba NA1500 CHN Combustion Analyzer (Carlo Erba Instrumentazione). Percent inorganic material was measured by filtering SFPM onto ashed glass fiber filters, drying at 60 °C for 2 days, weighing, ashing at 500 °C for 24 h and then reweighing to obtain ash free dry mass (AFDM) and % inorganic (100 * mg ash mass mg DM^{-1}). The proportion of leaves, diatoms, and other algae were measured using microscopy (Benke & Wallace, 1997). SFPM was filtered onto

0.45 μm filters (Gelman Corporation, Ann Arbor, MI); filters were cleared with immersion oil; the areal proportion of leaves, diatoms and amorphous detritus was measured using an imaging software (ImagePro©) connected to a microscope (100×). Animal material was infrequently detected and was excluded from analysis.

Regression analysis was used to determine if variables measured were related to catchment size. The extent of seasonal variability was determined by examining the spread of the samples from each season around the mean as indicated by the coefficient of variation (CV) for each site.

Growth experiment

Instantaneous growth rates of chironomids fed SFPM was used as an integrated measure of SFPM quality. Other studies have used chironomid growth as an indicator of food quality because of their short lifespan and rapid growth rates (Gresens, 1997, Meyer et al., 2000, Vos et al., 2000). Chironomids were collected from the LTR at the 7th-order site in April 1999 and placed in a cooler the day before the experiment was begun. Chironomids were removed from the rocks and individuals were haphazardly collected. Numerous chironomid taxa were present, although only non-tanypodinae (non-predatory) taxa were used for the experimental treatments (Merritt & Cummins, 1996).

Individuals were measured using an ocular micrometer (total length), and a single chironomid was placed in a sterile petri dish that contained 3–5 mg of thawed SFPM and 10 ml dechlorinated tapwater. Tests were done with chironomids prior to the experiment to insure that the amount of SFPM provided an adequate food supply. Sixteen treatments (4 sites * 4 seasons) were run concurrently using chironomids collected from a single pool of individuals. Twenty replicates (individuals) were used per treatment (resulting in 340 individuals total). Individuals of different sizes were distributed evenly across treatments to ensure that potential effects of size on growth rate would not affect the results. High replication allowed for adequate numbers for statistics given potentially high mortality from collection and handling injuries. The experiment was housed in an incubator at 16 °C in a 12/12 light/dark schedule. After five days, lengths of all the surviving individuals were measured again. Mortality and emergence were also recorded. Lengths were converted to biomass using regressions from Benke et al. (1999). Instantaneous growth rates (IGRs) of the individuals were calculated as follows (Waldbauer, 1968):

$$\mathrm{IGR}(\mathrm{d}^{-1}) = \frac{\ln \text{final mass} - \ln \text{initial mass}}{\text{days in interval}}.$$

After removal of the chironomids, subsamples of the SFPM were preserved in 2% formalin for later analysis of bacteria. Four subsamples were collected for bacteria analysis for each site and season. Samples were sonicated for 1 min to remove bacteria cells from the particles. Bacteria were stained with acridine orange and counted using an epifluorescence microscope (100× Olympus BH-2, Olympus Corp. Melville, New York) (Hobbie et al., 1977). A subsample of the solution was dried to measure DM per ml, and bacteria density per g DM of SFPM was then calculated. This method does not measure bacterial density associated with SPFM in the river; rather it provides data on the bacterial density associated with the SFPM in the chambers during the experiment.

IGRs were not normally distributed; therefore, a non-parametric test (Kruskal–Wallis Rank Sum) was used to determine if there were significant differences among sites and seasons. Regression analysis was used to determine which variables (% lipids, % diatoms, etc.) were related to growth rates. Principal Components Analysis (PCA) can be used to reduce a large number of variables, into a smaller set of linear combinations of the variables. PCA (on correlations) was used to reduce the traditional measures of quality down to a few principal components that encompass the variability in the measurements. Then we determined if the combinations of these variables were related to IGRs. Statistical analysis was conducted using JMP© (Version 3.2.6, SAS Institute) software.

Results

Composition of suspended fine particulate matter

SFPM along the Little Tennessee River continuum varied markedly. As catchment area increased, there was a trend of increased N/C of the particles (Fig. 2a). The seasonal variability of N/C also increased downstream; the coefficient of variation (CV): was 3.5% for the most upstream 5th order site, 24% for the second 5th-order site, 12% for the third site and 44% for the most downstream site. There was an increase in % inorganic matter with catchment area (Fig. 2b);

however, seasonal variability in % inorganic matter was consistent among sites, with CVs ranging from 10–17%. Percent diatoms were not related to catchment area (Fig. 2c), although % diatoms was highest during spring at the most downstream site (Fig. 2c). Seasonal variability in % diatoms was high at all sites with CVs ranging from 48–88%. Percent extractable lipids declined steadily downstream (Fig. 2d). The seasonal variability in % lipids was similar across all sites. Calories (cal g^{-1} DM) did not show a clear pattern among sites and did not show seasonal patterns (Fig. 2e). Bacteria density at the end of the growth experiment (#bacteria cells g^{-1} DM of SFPM) decreased slightly with catchment area (Fig. 2f). Seasonal variability decreased with catchment area; the CV of the most upstream 5th order site was 61%, the second 5th order site was 37%, the third site was 31% and the most downstream site was 23%.

Chironomid growth as a measure of SFPM quality

Percent mortality in the chironomid growth experiment ranged from 40–60% but was not significantly different among sites or seasons ($p = 0.31$), and there was minimal emergence (less than 10 for the entire experiment). Dead or emerged individuals were not included in the analysis. Despite mortality, the high replication (20 replicates per treatment) resulted in an adequate number of survivors for statistical analysis. Instantaneous growth rates were not significantly different among seasons for any site; therefore we used data from all seasons for each site to detect differences among sites. Instantaneous growth rates differed among sites (Kruskal–Wallis Rank Sum, $p = 0.025$) (Fig. 3) and IGR was related to catchment area ($p = 0.05$). This trend was most apparent in July. The instantaneous growth rates of the two 5th and the 6th order sites were not significantly different (Nemenyi test, $p > 0.05$); however, the 7th order site had significantly higher instantaneous growth rates than the first 5th order site (Nemenyi test, $p < 0.05$).

Relationships of SFPM attributes and growth

No single variable explained the variability in IGR (Table 2); however, % diatoms was weakly related to IGR. Principal component analysis (PCA) on correlations described the variability in the independent variables (% lipids, % inorganics, % diatoms, N/C and bacteria). Calories were excluded because of missing values. Two principal components were obtained that explained 55% and 23% of the variability (Table 3); hence, PCA was effective at reducing the five variables down to two variables which together explain 78% of the variability among the independent variables. The first PCA was most weighted by % lipids (negatively), N/C (positively) and % inorganic (positively). The second PCA was most weighted by % diatoms (positively) and bacteria (negatively). The first PCA was not related to IGR ($r^2 = 0.06$, $p = 0.80$), while the second PCA was weakly related to IGR ($r^2 = 0.18$, $p = 0.10$). This indicates that the combination of bacteria density at the end of the growth experiment (negative) and % diatoms (positive) explains some of the variability in IGR.

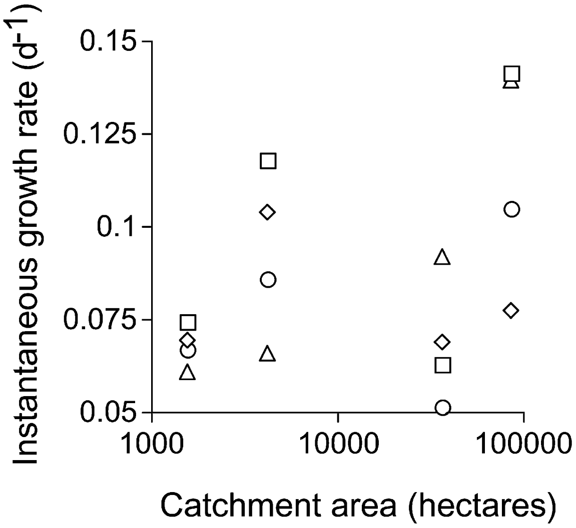

Figure 3. Mean instantaneous growth rates of chironomids fed suspended fine particulate matter collected from Coweeta Creek, Conley Road, Prentiss and Iotla in January (◇), May (○), July (△) and October (□) 1998.

Table 2. Relationships of traditional measurements of quality and the instantaneous growth rates measured.

Variable	r^2	p value
% Lipids	0.02	0.82
N/C	0.03	0.50
Calories	0.00	0.86
% Diatoms	0.14	0.16
Bacteria	0.00	0.77
% Inorganic	0.06	0.35

Table 3. Results from the principal components analysis. The percent of variability in the data set that can be attributed to each principal component (PC1 and PC 2) is indicated. A variable with a high eigenvector loading (absolute value) is one that is driving a large amount of the variability in the principal component.

	PC 1	PC 2
Percent of variance explained	55	23
Eigenvector loading		
% Lipids	−0.53	0.05
Nitrogen to carbon ratio	0.52	−0.21
% Diatoms	−0.11	0.87
% Inorganic	0.55	0.15
Bacteria	−0.36	−0.42

Discussion

These results do not support the RCC hypothesis that downstream reaches have more refractory compounds (Vannote et al., 1980), but rather suggest that SFPM is more labile downstream. Although there were differences in traditional measures of SFPM quality among the 3 upstream sites, these differences did not result in significant differences in growth rates among these sites. The differences between the first site and the large river site were great enough to result in significant differences in growth rate: the large river site had higher food quality. These results support our hypothesis that quality would increase downstream, as the highest quality SFPM was collected from the most downstream site. We did not find evidence to support our hypothesis that mid-orders would have greater seasonal variability in SFPM quality.

Percent mortality was not a useful indicator of quality. The high percent mortality in this experiment may be due to the abundance of *Rheotanytarsus* at the site where chironomids were collected. *Rheotanytarsus* are sensitive to changes in flow, and the conditions in the experimental chambers may have caused them to die. Chironomids were haphazardly selected for each treatment and there were no differences in percent mortality across treatments; therefore, mortality of *Rheotanytarsus* did not affect the overall conclusions.

Although % diatoms was weakly related to IGR, no single variable or combination of variables was effective at explaining the patterns in measured IGR. These results may be a consequence of failure to measure the appropriate variables. It is more likely that IGR, as an integrative measure, does not simply reflect the sum of the SFPM parts. The variables that were used to measure SFPM are analogous to multiple stressors, which other studies have shown are not necessarily additive (Schindler et al., 1996; Breitberg et al., 1999).

Numerous studies demonstrated that different types of foods (leaves, wood, diatoms, etc.) vary in quality as measured by growth rates or assimilation efficiencies (Anderson & Cummins, 1979; Fuller & Mackay, 1981; Pandian & Marian, 1986; Webb & Merritt, 1987; Fuller et al., 1988; Rosillon, 1988; Fuller & Desmond, 1997). In combination, however, the constituents of SFPM did not affect growth rates in relation to their proportions (Vos et al., 2000, this study). Insects encounter FPOM as a conglomerate of food types and cannot separate these food types before ingestion. Some components of the food resource may be beneficial, such as calories, % lipids, % diatoms, while others may be negative, such as % inorganics. The combination of these different components represents what the insects ingest. It is necessary to measure growth rates of insects fed naturally occurring particle mixtures (Vos et al., 2000) in order to accurately assess the quality of SFPM as a food resource. In this study, particles that organisms would encounter in the field were used to obtain an estimate of the quality of SFPM. The quality of suspended fine particles was higher at the most downstream site than the most upstream site in Little Tennessee River using chironomids as test organisms.

Food quality and secondary production

Increasing quality of SFPM may contribute to the increase in secondary production of filtering insects along the Little Tennessee River (Table 1) (Grubaugh et al., 1997). More than 70% of the dominant filterer's secondary production (hydropsychid caddisflies) was supported by the consumption of amorphous detritus (Rosi-Marshall & Wallace, 2002), which is an important component of SFPM. The observed increase in filterer secondary production (Grubaugh et al., 1997) could be the result of four factors: (1) increased temperature (Grubaugh et al., 1997), (2) increased quantity of SFPM downstream (Rosi-Marshall & Wallace, 2002), (3) increased habitat availability and (4) increased quality of SFPM (this study). The secondary production of filtering insects increased by two orders of magnitude at the most downstream site; however, temperature and FPOM quantity increased linearly

(Table 1). Therefore, temperature and FPOM quantity did not appear to be responsible for the substantial increase in filterer secondary production at the large river site.

The macrophyte *Podostemum ceratophylum* (L.) provides an ideal habitat for filtering caddisflies, as it is a stable structure for net construction (Grubaugh et al., 1997). The three most downstream sites all have *P. ceratophylum* on cobbles, but only the most downstream site has *P. ceratophylum*-covered bedrock as a dominant habitat (38%, compared to 0% at all other sites) (Table 1). The stability of *P. ceratophylum*-covered bedrock appears to be more important to filterer secondary production than *P. ceratophylum* on cobbles only.

In addition, the quality of SFPM was significantly higher at the downstream site. This suggests that filtering macroinvertebrates are able to exploit high quality habitat and thrive because a high quality food resource is constantly delivered by the flow of the river. Secondary production is an important ecosystem function (Benke, 1993), so it is noteworthy that it can be affected by food quality. Through SFPM's influence on the secondary production of its consumers, the food quality at a site could have repercussions throughout the food web, thereby affecting many more trophic levels than the initial consumer of the resource.

Suspended fine particles are a dominant food resource in southeastern river systems (Wallace et al., 1987; Couch et al., 1996; Hall & Meyer, 1998; Benke & Wallace, 1997; Rosi & Wallace, 2002), and the quality of this resource could have a significant effect on food webs in these river ecosystems. Anthropogenic factors that degrade or enhance this resource could have repercussions throughout the food web.

Acknowledgements

This work was supported by National Science Foundation grant DEB-9632854. Sue Eggert assisted with field work and Jeff Pollock counted bacteria samples. J. Bruce Wallace, Mary Freeman, Charles Jagoe, and two anonymous reviewers provided useful comments and suggestions.

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