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Characterization of Particulate Organic Matter Transported by Some Cascade Mountain Streams

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Field and laboratory studies were conducted to characterize concentrations, factors determining concentrations, particle size composition, and presumed food quality of particulate organic matter (POM) transported by streams of four different orders in Oregon's Cascade Mountains. Devils Club Creek (first order) and Mack Creek (third order) as high gradient, heavily shaded headwater streams receive large amounts of forest debris. Lookout Creek (fifth order) and the McKenzie River (seventh order) have lower gradients and more organic inputs from in situ aquatic primary producers and organic matter drifting from upstream areas than from the adjacent forest. Concentration of particulate organic matter is low during periods of nonstorm discharge, and not significantly related to stream power or type of organic input. All streams transport a mean POM particle size <12 μm. Over 70% of all particulate organic matter transported is very fine particulate organic matter (VPOM: 0.45–53 μm). Except for spring, the ratio of coarse (>1 mm) to fine (0.45 μm–1 mm) organic matter (CPOM:FPOM) is near zero, but remains elevated for the McKenzie River during all seasons. As determined by the amount of chlorophyll, carbon to nitrogen (C:N) ratio, percentage of organic matter and respiration rate, the presumed food quality of drifting organic matter is potentially better in downstream reaches.

Key words: food quality, detritus, organic matter, streams, rivers, watershed, drift, transport

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On a fait des études sur le terrain et au laboratoire dans le but de déterminer les concentrations, les facteurs responsables de ces concentrations, la grosseur des particules et la qualité nutritive présumée de matériaux organiques particulaires (POM) transportés par des cours d'eau de quatre ordres différents dans les montagnes Cascades de l'Orégon. Le ruisseau Devils Club (premier ordre) et le ruisseau Mack (troisième ordre), cours d'eau à gradient prononcé et à tête très ombragée, reçoivent de grandes quantités de débris forestiers. Le ruisseau Lookout (cinquième ordre) et la rivière McKenzie (septième ordre) ont des gradients moins prononcés et reçoivent de plus grands apports de matière organique des producteurs primaires aquatiques *in situ* et de matière organique dérivante en provenance des régions d'amont qu'ils n'en reçoivent de la forêt avoisinante. La concentration de matières organiques particulaires est basse durant les périodes de débit autres que les débits d'orages, et n'est pas nettement liée à la force du cours d'eau ou au type d'apport organique. Tous les cours d'eau transportent des POM de grosseur inférieure à 12 μm. Plus de 70% de toute la matière organique particulaire transportée est une matière particulaire très fine (VPOM : 0,45 à 53 μm). Sauf au printemps, le rapport des matières organiques grossières (>1 mm) aux matières fines (0,45 μm à 1 mm) (CPOM:FPOM) se rapproche de zéro, mais demeure élevé dans la rivière McKenzie à toute saison. A en juger par la quantité de chlorophylle, le rapport carbone:azote (C:N), le pourcentage de matières organiques et le taux de respiration, la qualité nutritive présumée des matières organiques dérivantes est potentiellement supérieure dans la partie inférieure des cours d'eau.

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TRANSPORT of organic detritus by streams and rivers is a conspicuous component of their ecosystem structure but has never been adequately characterized for potential food quality, relative proportions of size fractions, or basic differences inherent between stream orders in a given watershed. Transport of organic detritus in streams and rivers is important to invertebrates, especially the filter feeders (Cummins 1974; Wallace et al. 1977), and can be of considerable significance to estuarine communities (Naiman and Sibert 1978). By contrast, drift of living organisms in streams is better documented (Waters 1969).

Studies of drifting organic detritus have been mostly concerned with concentrations of the dissolved (<0.45 μm) and particulate (>0.45 μm) fractions, and only a few studies address an entire year (Fisher and Likens 1973; Hobbie and Likens 1973; Brinson 1976; Naiman 1976; Liaw and MacCrimmon 1977). Other studies have microscopically examined downstream variations in the structure of drifting organic detritus (Egglishaw and Shackley 1971), while the origin and fate of plankton in streams has been examined by Chandler (1937), Maciolek and Tunzi (1968), and Swanson and Backmann (1976). The role of filter feeders in streams, and their food, was recently reviewed by Wallace et al. (1977). Seki et al. (1969), Stephens et al. (1967), and Naiman and Sibert (1978) studied the importance and fate of stream inputs of organic material to coastal environments. Vannote has theorized on the ratio of coarse to fine organic detritus in relation to stream order (Cummins 1975, 1977), but only Sedell et al. (1979) have attempted to relate concentrations to physical factors.

In this paper we characterize drifting organic detritus in four streams of different order in Oregon's Cascade Mountains. We examine by size fraction, concentrations, percentage organic matter, carbon to nitrogen (C:N) ratio, chlorophyll *a*, and respiration rate. We test the hypothesis that coarse particulate organic matter (CPOM: >1 mm) is not an important component of drifting organic matter in very small (first order) streams, becomes increasingly important in slightly larger (second–third order) streams where greater power is available to move larger particles, and then decreases in importance in larger streams as abiotic–biotic processing is completed (Cummins 1975, 1977). We also attempt to relate concentrations of particulate organic matter (POM) to unit stream power and presence of retention structures. Finally, we examine the postulate that the overall food quality of drifting organic matter is better in downstream reaches.

Study Area

The H. J. Andrews Experimental Forest (6000 ha, 60 km^2) in Oregon's Cascade Mountains is characterized by high gradient streams, a maritime climate, and distinct seasonal rainfall. All streams experience autumn and spring freshets and low summer flows. Annual precipitation ranges from 225 cm at lower elevations to 350 cm on the ridges. High elevations have extensive snow packs during winter, while rain predominates at lower elevations (Berntsen and Rothacher 1959). Dominant forest vegetation is Douglas fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and alder (*Alnus rubra*) along the lower elevation streams. Three of the four study sites (Devils Club Creek, Mack Creek, and Lookout Creek) are within the Andrews Forest, and one (McKenzie River) is adjacent to the forest.

Devils Club Creek is a first order stream (Strahler 1957) (Table 1, Fig. 1). The stream channel is choked with coarse organic debris derived from windfall Douglas fir (≈400 yr old) accumulated over the last several hundred years, and leaf fall from huckleberry (*Vaccinium parvifolium*), devils club (*Oplopanax horridum*), maple (*Acer macrophyllum* and *Acer circinatum*), and Douglas fir needles (Naiman and Sedell unpublished data). Autochthonous production is extremely low (Naiman and Sedell unpublished data) in this heavily shaded stream which discharges directly into Mack Creek.

Mack Creek is one of three major streams draining the Andrews Forest (Table 1, Fig. 1). The morphology of this third order stream is characterized by a stairstep of gouged pools, free fall zones, and turbulent water around large boulders. Substrate ranges from large boulders to sand but is mostly loose cobble (Sedell et al. 1975). Woody debris is prevalent but much less concentrated than in Devils Club Creek. In Mack Creek the forest canopy opens slightly, allowing light flecks to reach the stream. There is some primary production by microalgae but it is still not a major organic input (Gregory 1978; Naiman and Sedell unpublished data). Windborne debris, lateral movement from steep side slopes, and downstream transport from tributaries are the primary biological inputs. Mack Creek is a major tributary of Lookout Creek.

Lookout Creek receives runoff from the entire Andrews Forest (Table 1, Fig. 1). This fifth order stream consists of shallow riffles interspersed with small pools; the substrate is large cobbles and bedrock. There is little woody debris in the stream, the canopy is open, and most daily sunlight reaches the extensive periphyton community (Naiman and Sedell unpublished data). Primary production by diatoms, filamentous algae, and stream lettuce (*Prasiola*), as well as transport from upland areas, are the major organic inputs. Allochthonous input from leaf fall is important only in late summer and autumn when maple leaves and conifer needles reach the stream. Lookout Creek discharges into Blue River which, in turn, is a tributary of the McKenzie River.

The McKenzie River is a seventh order stream draining the western Cascade Mountains (Table 1, Fig. 1). Morphologically, it is 85% riffle-runs with few alcoves or pools. Substrate is cemented cobble and large boulders; significant woody debris has not accumulated. Alder and Douglas fir along stream margins contribute some organic matter but most inputs are from downstream transport, periphyton production, and aquatic macrophytes. A zone of aquatic mosses (*Fontinalis* sp.) extends 5 m from both banks. There is a moderate to dense periphyton community over the entire substrate (Naiman and Sedell unpublished data).

Autochthonous and allochthonous inputs, the immediate sources of drifting organic matter, vary widely in amount and composition for each study site (Naiman and Sedell unpublished data). Once inputs reach the stream they have

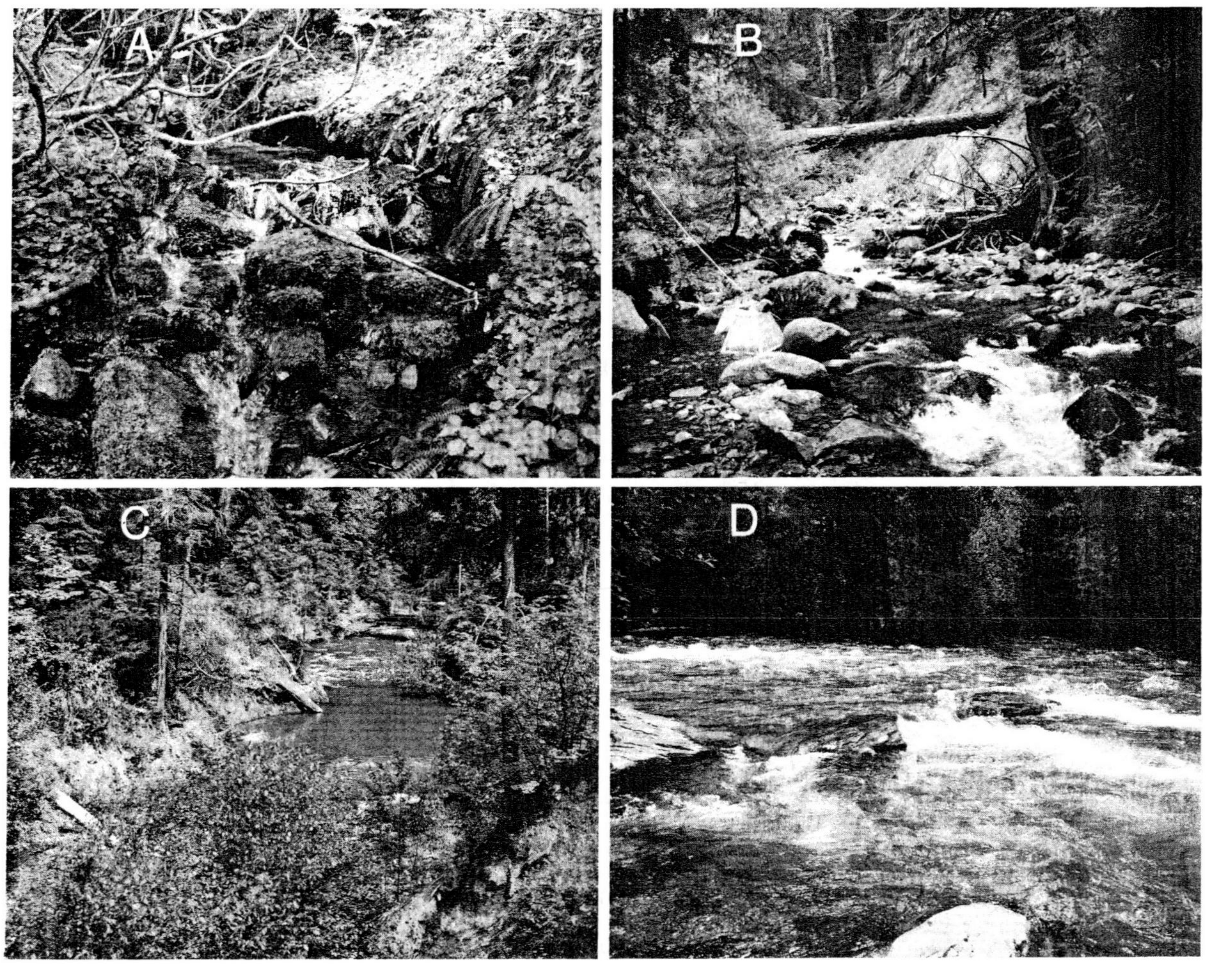

FIG. 1. A, Devils Club Creek; B, Mack Creek; C, Lookout Creek; D, the McKenzie River.

the potential to drift immediately or be retained and processed in place. Each biological input will show a different propensity for drifting and abiotic–biotic processing rates depending upon composition, temperature, water chemistry, stream flow, and stream morphometry. In general, all Andrews Forest sites have similar temperature regimes with winter lows of about 1°C and summer maxima of about 15–18°C, and similar water chemistry (Table 2). The McKenzie River, however, has a narrower temperature range varying from about 3°C in winter to 12°C in summer, and a slightly different water chemistry with higher concentrations of phosphorus, lower concentrations of nitrogen, and slightly higher alkalinity. All four sites are quite different in stream flow and morphometry (Table 1).

Materials and Methods

We sampled during periods of normal seasonal flow in March (winter), May (spring), July (summer), and October (autumn) in 1976, and in February (winter) 1977. Unusual events (freshets) were not sampled because they were judged not to be of immediate importance to the biological community, although freshets are of great importance in the redistribution of organic matter.

Organic drift $>106\ \mu m$ was estimated at all sites with Miller high speed plankton samplers. In Devils Club Creek either the entire stream was diverted through the sampler, or at high flows, a substantial portion of the stream was channeled by a hose into the net. Nets in Devils Club Creek

TABLE 1. Physical characterization of sampling locations.

Parameter	Devils Club Creek	Mack Creek	Lookout Creek	McKenzie River
Mean width (m)	0.6	3.0	12.0	40.0
Mean depth (m)	0.05	0.22	0.90	1.60
Discharge ($L \cdot s^{-1}$):				
Maximum	14.0	825	8 462	115 000
Mean Annual	1.7	92	377	75 300
Minimum	0.3	25	258	13 500
Stream gradient (%)	40.0	13.0	3.0	0.6
Watershed area (km^2)	0.2	6.0	60.5	1 024.0
Stream length (km)	0.5	3.2	14.4	57.6
Stream length / Watershed area ($km \cdot km^{-2}$)	5.00	0.72	0.22	0.06
Freshets per year				
5x Base flow	32	12	6	0
10x Base flow	13	5	2	0
Stream order	1	3	5	7
Elevation (m)	810	800	420	410
Benthic detritus ($g\ AFDW \cdot m^{-2}$)	117 677	15 393	123	84

TABLE 2. Summary of water chemistry for sampling site by season ($mg \cdot L^{-1}$). TDS = Total dissolved solids ($mg \cdot L^{-1}$).

Season	Location	Total P	Ortho P	NH_3-N	NO_2-N	NO_3-N	Total N	TDS	Hardness	Alkalinity ($mmol \cdot L^{-1}$)	Sample size (*n*)
Winter	Devils Club Creek	0.0361	0.0039	0.0109	0	0.0235	0.0298	42.3	9.8	0.105	3
	Mack Creek	0.0279	0.0080	0.0022	0	0.0222	0.0273	36.0	10.1	0.092	3
	Lookout Creek	0.0429	0.0096	0.0069	0	0	0.0227	30.5	9.7	0.013	2
	McKenzie River	0.0670	0.0327	0.0072	0	0	0.0072	34.5	15.3	0.190	4
Spring	Devils Club Creek	0.0231	0.0109	0.0011	0	0.0003	0.0230	50.3	12.4	0.063	4
	Mack Creek	0.0150	0.0058	0	0	0.0760	0.0295	36.3	8.2	0.056	4
	Lookout Creek	0.0261	0.0073	0.0034	0	0.0327	0.0284	36.0	8.1	0.066	4
	McKenzie River	0.0528	0.0282	0.0032	0	0.0042	0.0247	47.3	14.3	0.167	4
Summer	Devils Club Creek	0.0176	0.0120	0.0264	0	0.0006	0.0278	89.2	14.6	0.129	5
	Mack Creek	0.0150	0.0104	0.0090	0	0.0238	0.0252	87.2	11.0	0.107	5
	Lookout Creek	0.0150	0.0108	0.0059	0	0.0054	0.0272	98.2	12.4	0.131	5
	McKenzie River	0.0404	0.0342	0.0012	0	0.0010	0.0108	95.6	15.6	0.197	5
Autumn	Devils Club Creek	0.0284	0.0128	0.0265	0	0.0006	0.0298	4.9	13.9	0.137	5
	Mack Creek	0.0304	0.0124	0.0025	0	0.0034	0.0224	5.2	13.0	0.132	5
	Lookout Creek	0.0326	0.0154	0.0032	0	0.0432	0.0246	5.8	13.0	0.055	5
	McKenzie River	0.0630	0.0496	0.0011	0	0.0026	0.0044	6.5	17.0	0.244	5

TABLE 3. Average seasonal concentration (mg AFDW·m^{-3}) of drifting particulate organic matter and the diel coefficient of variation (CV, %) is calculated for each stream.

	Mean particulate transport							
	Devils Club Creek		Mack Creek		Lookout Creek		McKenzie River	
Season	$\bar{x}$	CV	$\bar{x}$	CV	$\bar{x}$	CV	$\bar{x}$	CV
Winter	1347.4	13.9	1266.9	20.7	1102.8	29.3	681.9	7.6
Spring[a]	539.1	0.2	212.3	3.2	309.0	2.1	918.8	2.2
Summer	1078.5	4.3	461.6	7.7	455.9	0.9	751.3	1.4
Autumn	900.3	16.6	425.6	19.2	447.4	24.5	615.7	27.1
Mean	966.3	8.8	591.6	12.7	578.8	14.2	741.9	9.6

[a]53–106 μm not sampled.

were left in place for 4–14 h over 1–3 d each season. Organic matter transported in Mack Creek, Lookout Creek, and the McKenzie River was sampled for various times up to an hour, 4–8 times at equal intervals over a diel period for 1–3 d each season. The nets were not allowed to clog with debris.

Concentrations in milligrams AFDW per cubic metre were estimated, after any large invertebrates were removed, by dividing the ash-free dry weight (AFDW) of the sample by the estimated volume of water filtered by the nets. The volume of water sampled was determined with fluorescent dyes and is accurate to ±5%. Dyes were injected into the mouth of the sampler and the time taken to pass through recorded. These data were combined with sampler volume to estimate volume of water filtered. All material taken in the Miller sampler was sorted into size-classes of >16 mm, 16–4 mm, 4–1 mm, 1 mm–500 μm, 500–250 μm, and 250–106 μm. Concentration of particles between 53 and 106 μm was determined by filtering 200 L of water through a 53-μm screen. This was done twice in spring and 12 times over 1–3 d for other seasons for all sites. For particles in the 0.45–53-μm size fraction, 15–20 L of water was first sieved through a 53-μm net and then filtered onto a preweighed and precombusted (550°C, 2–4 h) Gelman glass fiber filter until it clogged. The total volume filtered was noted. This size fraction was estimated only 1–3 times in spring and 10–12 times, during a 1-3-d period, for the remaining seasons. For winter samples this size fraction was further subdivided into 5.0–53 μm and 0.45–5.0 μm. Water was sieved through a 53-μm net and filtered through a 5.0-μm nucleopore filter. Water passing through this filter was passed through a Gelman glass fibre filter.

To facilitate comparison with other studies we defined coarse particulate organic matter (CPOM) as particles >1 mm diam; fine particulate organic matter (FPOM) as >0.45 μm–1 mm diam; and very fine particulate organic matter (VPOM) as 0.45–53 μm (Boling et al. 1975).

The amount of material transported by streams is partially a function of stream power. Unit stream power is an indication of the ability of water to move particles and can be estimated from the equation $\omega = \rho Qs/w$ where ω is power per unit width (kg·m^{-1}·s^{-1}), Q is discharge in cubic metres per second, s is slope in percent, width (w) is in metres, and ρ is the density of water (Leopold et al. 1964). This is the work rate of flowing water per unit width of stream.

To investigate food quality a large sample of drifting organic detritus was collected from each site, divided into the eight size-classes, and the invertebrates removed. A portion of each size-class was used for chlorophyll *a*, respiration, and carbon to nitrogen (C:N) ratio estimates. Chlorophyll *a* per milligram of AFDW, corrected for phaeophyton, was estimated by extraction in 10 mL of 90% acetone for 24 h (Strickland and Parsons 1972) and the use of a Beckman spectrophotometer. After chlorophyll extraction, detritus was weighed and ashed at 550°C. Respiration was determined at our streamside laboratory with a Gilson respirometer at ambient stream temperatures (Gilson 1963). Four to six respiration estimates were made for each size-class where enough material could be collected. Samples were then ashed and weighed. C:N was determined with a Carlo Erba Elemental Analyser. Samples were dried and divided into two portions; one was used for C:N analysis and the other ashed.

Results and Discussion

CONCENTRATIONS

On an annual basis Devils Club Creek exports the highest concentration of particulate organic detritus of the four streams; the McKenzie River transports the next highest level (Table 3). Mack Creek and Lookout Creek have the lowest concentrations. The three Andrews Forest sites have similar seasonal patterns; highest concentrations are in winter and lowest concentrations during autumn when flow is minimal. The McKenzie River transports the highest concentration during spring snowmelt and lowest in early autumn.

Variations within a day are small compared to the mean transport concentration; coefficients of variation (CV) range from only 0.2% in Devils Club Creek to 29.3% in Lookout Creek (Table 3). CVs are least in spring and summer and greatest during autumn and winter. Diel variations in organic matter concentration are, however, neither regular nor of sufficient magnitude to be considered periodic.

Concentrations of organic matter transported by unaltered coniferous forest streams are usually low when compared to other streams (Sedell et al. 1979). Among

TABLE 4. DOC:POC by site and season. Mean seasonal concentration of drifting POM is assumed to be 50% carbon.

Season	Devils Club Creek	Mack Creek	Lookout Creek	McKenzie River
Winter	1.76	2.59	2.60	1.61
Spring	4.43	8.57	3.73	1.38
Summer	3.14	4.43	2.46	1.37
Autumn	4.53	6.47	7.63	2.70

TABLE 5. Average unit stream power ($\bar{x}$) calculated for each sampling date by site and season. Standard deviations are all ≤ 0.01.

Season	Devils Club Creek	Mack Creek	Lookout Creek	McKenzie River
Winter	0.07	0.17	0.12	0.56
Spring	0.40	1.14	1.26	1.46
Summer	0.07	0.27	0.15	0.84
Autumn	0.03	0.12	0.09	0.68

the more important factors contributing to the low levels are the following: efficient retention and processing by the forest and its streams, inputs of large CPOM not easily moved by currents, low nutrient concentrations limiting the development of a large biomass of primary producers, and fast currents or high precipitation eroding the stream bed to cobble or bedrock. These and other influences interact to produce the remarkably clear waters typical of western Oregon and other areas with unaltered coniferous forest streams. Where some of these factors are not as pronounced, considerable amounts of fine detritus and primary producers can accrue, contributing to higher transport concentrations.

DOC:POC RATIO

Dissolved organic carbon (DOC: $<0.45\ \mu$m) concentrations, as measured by persulfate oxidation (S. V. Gregory unpublished data), are usually less than an order of magnitude larger than the mean seasonal POC ($>0.45\ \mu$m) concentrations (Table 4). In all cases the DOC:POC ratios range from 1 to 9, being lowest in the McKenzie River and during winter for all sites.

According to Wetzel and Rich (1973), the DOC:POC ratio normally ranges from 6 to 10 in lakes and rivers, with lower ratios reported mostly from highly productive lake waters. Malcolm and Durum (1976) have reported DOC:POC ratios ranging from approximately 1 to 18 for a variety of rivers. Ratios for our sites fall into this latter range.

STREAM POWER

The amount of organic material transported by stream is partly a function of stream power. Unit stream power is a measure of a streams' ability to do this work.

mediate, and of nearly equal magnitude, in Mack Creek and Lookout Creek (Table 5). At each site, among the days sampled each season, there is little change in unit stream power. However, due to seasonal differences in discharge there is a considerable difference in unit stream power among seasons, with highest values in spring and lowest in autumn.

We are unable, however, to show a significant relationship between POM concentrations and unit stream power ($r = -0.03$, $P = 0.75$, $n = 114$), or between mean seasonal concentrations and unit stream power ($r = -0.41$, $P = 0.06$, $n = 16$) (Fig. 2). POM concentrations do not significantly respond to changes in stream power alone; however, closer examination suggests that concentration decreases with increasing unit stream power with the Andrews Forest (i.e. excluding the McKenzie River site).

Unit stream power, by itself, is not a good predictor of POM concentrations transported within a watershed, although Sedell et al. (1979) found it to be a fairly useful tool for comparisons between streams with different watershed characteristics. Organic matter concentrations within a biome watershed tend to remain within an order of magnitude. There are several factors determining that magnitude: types and amounts of organic inputs, stream power, number and type of retention structures, and frequency of flood recurrences. The flood recurrence interval for all sites is 1.2 yr. As yet, however, we have been unable to quantify all physical, chemical, and biological retention structures in these streams and determine their relation to the amount of particulate organic matter being transported. Stream power moves materials downstream while retention structures resist this movement. The interaction between these factors is of considerable importance in determining both the amount and size distribution of

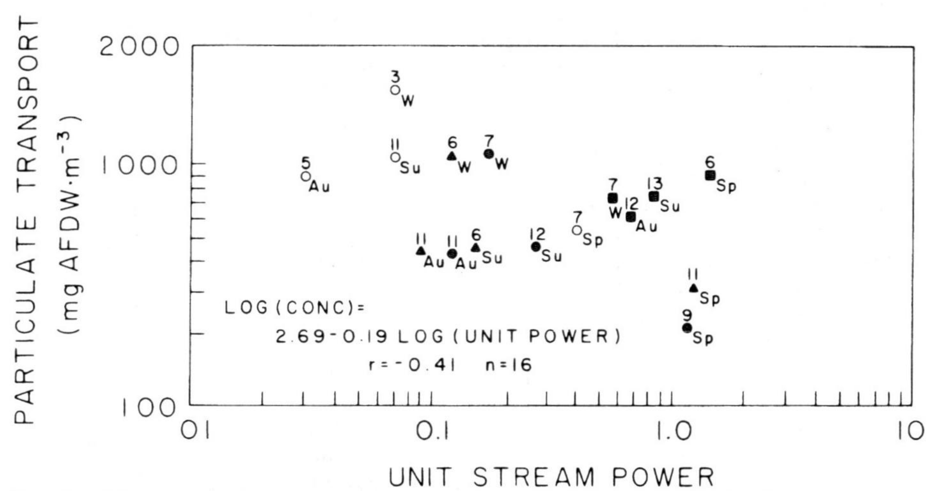

FIG. 2. Mean particulate organic matter concentrations and sample size for a season are shown as a function of unit stream power. Coefficient of variation for each power data point is <5%. ○, Devils Club Creek; ●, Mack Creek; ▲, Lookout Creek; ■, McKenzie River; W, Winter; Sp, Spring; Su, Summer; and Au, Autumn.

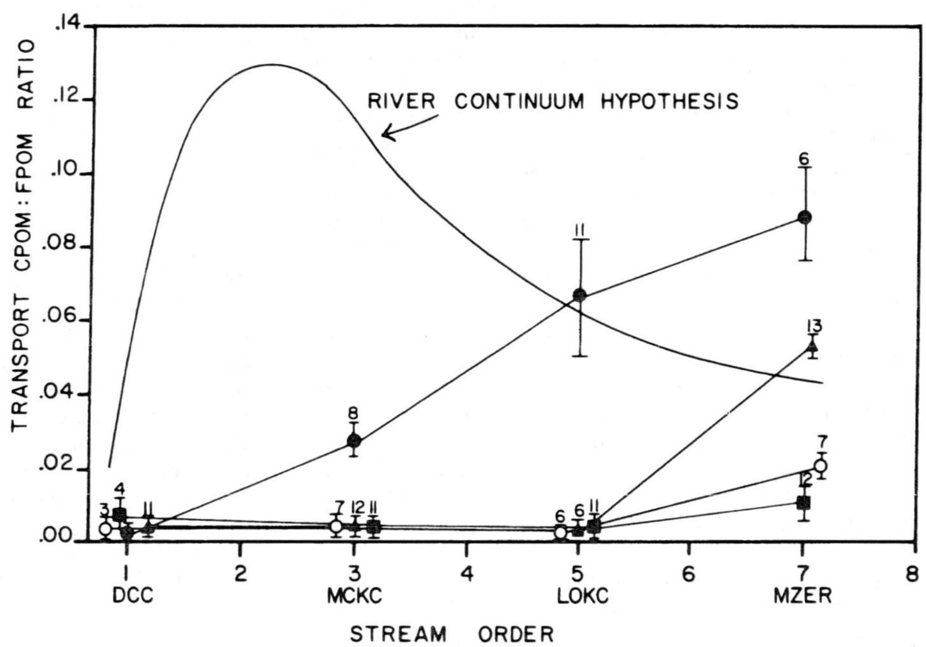

FIG. 3. CPOM:FPOM ($\bar{x} \pm$ SE, n) is shown as a function of stream order for each site and season. CPOM:FPOM values on the y-axis do not necessarily correspond to the conceptual hypothesis shown. ○, Winter; ●, Spring; ▲, Summer; ■, Autumn.

storms or whether samples are taken on a rising, falling, or stable hydrograph, will also greatly affect organic matter concentrations (Bilby and Likens 1979).

CPOM:FPOM

Vannote's River Continuum concept predicts CPOM:FPOM will decrease as stream order increases beyond the very small headwater streams that are nor- (Cummins 1975, 1977). The rationale is that small, heavily shaded forest streams receive more inputs of large organic particles in the form of wood and leaves, while large particle inputs are less important, and small organic particles relatively more important, in higher order streams. Our data are sufficient to test this concept both among stream orders and seasons. We found the concept not to be true for these four streams (Fig. 3). In spring, however, CPOM:FPOM increases with

($r = 0.99$; $P < 0.01$). In winter, summer, and autumn, however, CPOM:FPOM approaches zero for the Andrews Forest sites, remaining only slightly higher for the McKenzie River.

Between sites the average CPOM:FPOM increases with stream order. Although there is not a statistical difference, Devils Club Creek is always the lowest and the McKenzie River highest. This probably indicates that low order streams are efficient in retaining and processing organic inputs, whereas larger order streams are not quite as effective in retaining larger particles. This can be explained, in part, by stream power and retention characteristics.

CPOM:FPOM is dependent upon the physical size of biological inputs, stream power available to move organic material and the ability of retention structures to slow downstream movements of those inputs. Vannote (in Cummins 1975, 1977) takes into account the physical size of organic inputs but does not consider power or retention structures. Although Devils Club Creek and Mack Creek have inputs of predominantly woody debris and leaves, they also have efficient retention structures to retain coarse inputs against stream power and process them in place. Should the retention structures be altered or removed, as during some logging operations, a shift in CPOM:FPOM should be readily apparent with large amounts of coarse materials being moved downstream. This happened in an experimentally clearcut watershed in the Andrews Forest (Sedell unpublished data). Little downstream transport of organic material occurred when the old-growth forest was intact but after the watershed was logged, and normal stream debris increased, huge amounts of CPOM were exported. The increase in stream debris should not be equated with an increase in permanent retention structures which would slow CPOM movement. The McKenzie River normally exports relatively large amounts of CPOM, derived mostly from vegetation along its own stream margins rather than upstream tributaries, as a result of a few retention structures and high stream power. CPOM has few places to become lodged and hence tends to readily drift.

If transport of organic detritus is to be predictable, biological inputs, stream power, retention structures, and discharge patterns must be considered as interacting variables. Stream order by itself is not a good indicator of CPOM:FPOM, since all streams export mostly small-sized particles and many larger sized particles when retention structures are absent or altered.

Percentage Composition

As reported in Sedell et al. (1979) size fractions plotted as a cumulative percentage by weight reveal an interesting feature (Fig. 4). For all sites, in all seasons, the mean particle size of organic detritus in transport is between 3 and 12 μm. Larger particles (>106 μm) may be a visually conspicuous component of the drift at times; nevertheless, the majority of the organic drift is always less than about 12 μm.

During normal flow Devils Club Creek exports little organic matter >106 μm (Table 6); on an annual basis it accounts for only 5% of the drift. During spring Mack Creek and Lookout Creek export 17 and 14%, respectively, of total transport in the >106-μm fraction. At other times this fraction makes up <5% of the total. During spring and summer, particle sizes >106 μm make up 13 and 12% of the total in the McKenzie River but, surprisingly, are insignificant in autumn during leaf fall. For all sites, and all seasons, more than 70% of organic particulate drift is VPOM (0.45–53 μm) (Table 6).

TABLE 6. Percentage composition, by weight, of drifting particulate organic matter.

Location	Season	Percentage of total transport >106 μm	53–106 μm	0.45–53 μm
Devils Club Creek	Winter	5.3	8.5	86.2
	Spring[a]	1.2	—	98.8
	Summer	5.0	20.4	74.2
	Autumn	9.9	19.1	71.0
	Mean	5.45	16.0	82.6
Mack Creek	Winter	4.2	11.8	84.0
	Spring[a]	16.8	—	83.2
	Summer	9.1	16.1	74.8
	Autumn	4.2	6.0	89.8
	Mean	8.6	11.3	83.0
Lookout Creek	Winter	1.2	0.6	98.2
	Spring[a]	13.8	—	86.3
	Summer	4.7	6.1	89.3
	Autumn	1.3	9.7	89.1
	Mean	5.3	5.5	90.7
McKenzie River	Winter	8.0	7.5	84.6
	Spring[a]	18.2	5.7	76.2
	Summer	12.4	8.6	79.0
	Autumn	2.8	7.0	90.2
	Mean	10.4	7.2	82.5

[a] 53–106 μm not sampled.

The fact that low order streams export >70% of particulate organic matter as VPOM suggests the possible high efficiency of small stream systems in retaining and processing organic inputs. Unaltered small streams appear to have efficient retention structures to trap inputs, allowing them to be processed. Higher order streams transport mostly VPOM since a major biological input is VPOM from upstream areas and FPOM from local periphyton and macrophytes.

It is interesting, nonetheless, that each site and season has the same mean particle size in transport and that size is always small (3–12 μm). Recent studies

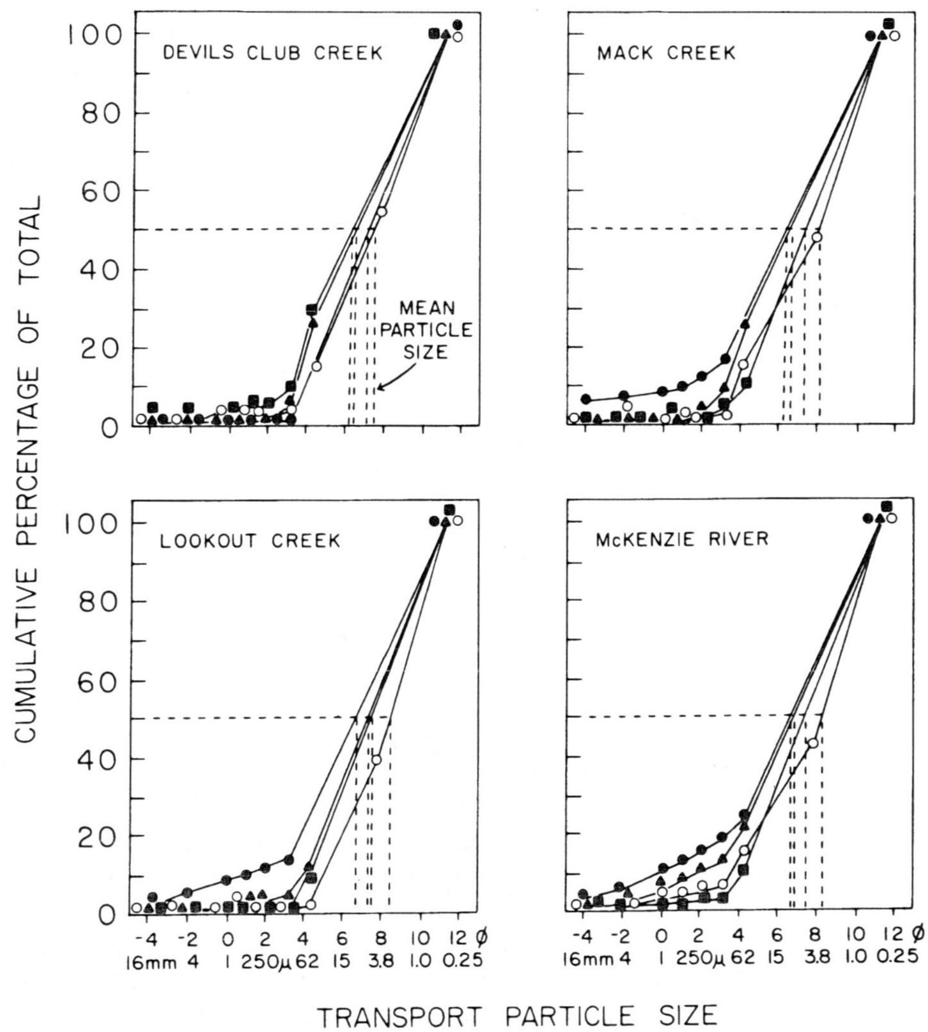

FIG. 4. Cumulative percentage of total organic drift (by weight) is shown as a function of particle size (both mm and ϕ [phi] units) for the sampling locations each season. Mean transport particle size is determined directly from the graph. $\phi = -\log_2$ (particle size, mm).

indicate many streams and rivers in a variety of watersheds transport most organic matter in the 3–20-μm size range. Seki et al. (1969) found the mean particle size for drifting organic matter in the Nanaimo River, British Columbia, to be 4 μm in summer and 20 μm in winter. Naiman (unpublished data) found the mean size range for 10 stations and all major tributaries of the Amazon River between Manaus, Brazil, and Iquitos, Peru, during the onset of flooding to be 3–15 μm.

This, however, does not explain why small particles are so abundant. In reality there seem to be only two possibilities (or a combination of both) to explain this observation. First, VPOM may be abundant because no organisms utilize it, or second, VPOM may be generated rapidly and continuously. It is a size range that can be generated from the processing of CPOM and FPOM, as well as from flocculation of DOM.

Not surprisingly there are invertebrate species adapted for feeding on drifting detritus particles in the VPOM size range (Wallace et al. 1977). Some Trichoptera have nets with mesh sizes to trap particles from 1 to 40 μm diam. Particles of this size range have been found in their guts, guts of many other Trichoptera species with larger mesh nets, and *Corbicula* clams (Wallace et al. 1977). Maciolek and Tunzi (1968) estimated that 60% of the cellular microalgae from a small California lake was removed within 0.4 km after entering a stream by filter feeding Simuliidae. These studies indicate the importance of VPOM to downstream communities and that particle sizes are selectively utilized; therefore, VPOM must be generated continuously and probably fairly rapidly.

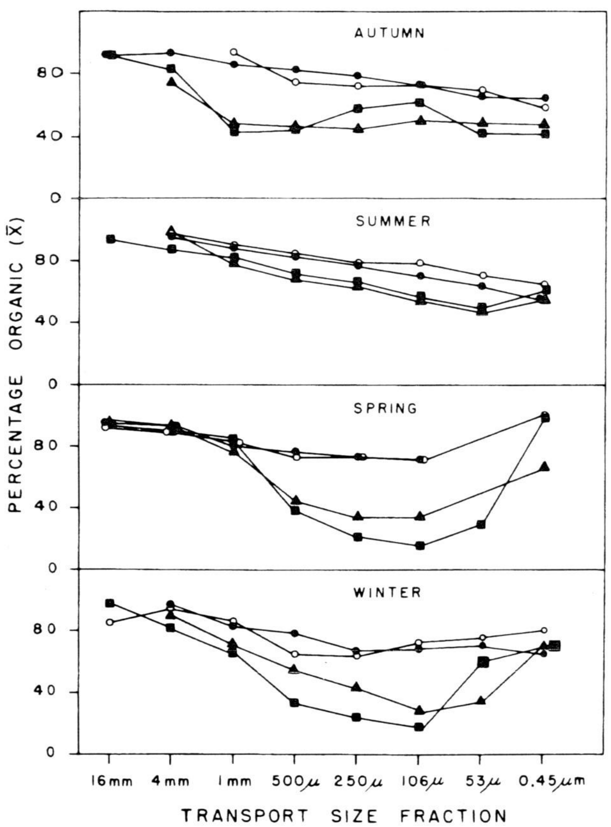

FIG. 5. Percentage organic matter is shown as a function of particle size by season for Devils Club Creek (○), Mack Creek (●), Lookout Creek (▲), and the McKenzie River (■).

Food Quality Studies

Food quality is defined as growth producing nutritive content per unit of food intake, whereas food quantity is defined as density per unit of environment (Cummins 1974; Ward and Cummins 1978). Food quantity and quality are obviously important in determining the distribution and abundance of invertebrate consumers and may be important in determining processing efficiencies. However, no criteria have been established for determining the quality of drifting organic matter. As a first analysis we examined percentage organic, chlorophyll *a*, C:N, and respiration rates associated with particles from the various size-groups.

Percentage organic — There are distinct differences in the percentage of organic matter among size-classes both between seasons and sites (Fig. 5). In general, percentage organic matter decreases as particle size decreases but may increase again in the 0.45-μm size-class. For sizes >1 mm the percentage of organic matter is normally >80% but decreases, depending on season and site, as particle size decreases.

The sharpest decrease in organic content with decreasing particle size is during spring and winter; summer has the slowest decline (Fig. 5). Rate of decline can also be grouped by site. Lookout Creek and the McKenzie River have the same general pattern for all seasons with a low organic content in the middle size-classes (53 μm–1 mm), while Devils Club Creek and Mack Creek show similarity in having relatively high percentage organic for all size-classes. Thus, small particle sizes are richer in organic material in low order streams than corresponding sizes in higher order streams. This could have a significant effect upon invertebrate communities in that search time for organic particles and clogging of feeding apparatus would be minimized in an environment with sufficient organic particles and few inorganic particles.

Chlorophyll — The percentage of total drifting organic material as chlorophyll *a* is estimated only for winter, summer, and autumn (Fig. 6). Organic matter concentrations are converted to carbon using empirical data and assuming a carbon:chlorophyll *a* conversion factor of 120 (Gregory 1978). Chlorophyll associated with VPOM is mostly from diatoms and microalgae while, in larger size-classes (>106 μm), it is mostly derived from leaves and needles.

There are distinct differences in the percentage of transport occurring as chlorophyll by size-class and by site, but only slight differences by season. As would be expected, the heavily shaded, lower order streams (Devils Club Creek and Mack Creek) export essentially no chlorophyll as diatoms or microalgae (Fig. 6). In Lookout Creek and the McKenzie River periphyton is abundant and contributes a relatively large percentage of the total organic matter transported (up to 92% in the McKenzie River).

Chlorophyll associated with leaves and needles is important in the McKenzie River and Lookout Creek, but of minor importance in Mack Creek. With the exception of a single input of huckleberry leaves, it is also of minor importance in Devils Club Creek. The middle size-classes (106 μm–1 mm) usually contain little chlorophyll since material in this size range is derived from decomposition of wood, leaves, needles, and mosses with nearly all chlorophyll degraded during the decomposition process.

In Lookout Creek and the McKenzie River greatest chlorophyll export is in autumn; periphyton has reached maximum biomass over the summer, is beginning to slough and, concurrently, autumn leaf fall is in process. Devils Club Creek and Mack Creek transport such small quantities of chlorophyll that seasonal differences are not apparent.

Respiration — Respiration was measured for as many particle sizes as possible in winter, summer, and autumn (Fig. 7). Water temperatures within sites are often different between seasons, but we could not demonstrate a significant relationship ($P > 0.05$) between stream

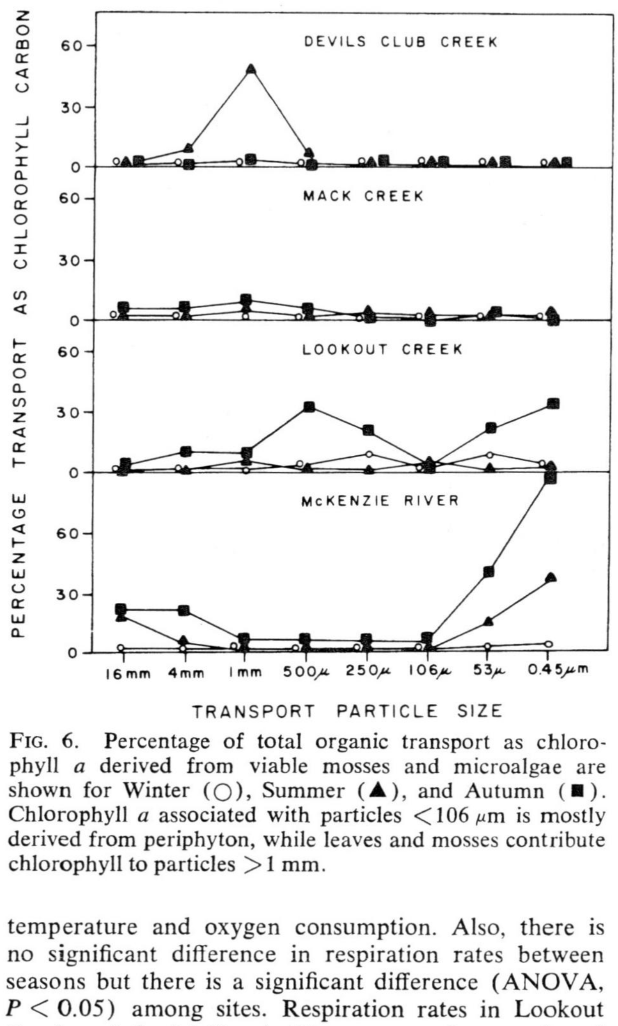

FIG. 6. Percentage of total organic transport as chlorophyll *a* derived from viable mosses and microalgae are shown for Winter (○), Summer (▲), and Autumn (■). Chlorophyll *a* associated with particles $<106\ \mu m$ is mostly derived from periphyton, while leaves and mosses contribute chlorophyll to particles >1 mm.

temperature and oxygen consumption. Also, there is no significant difference in respiration rates between seasons but there is a significant difference (ANOVA, $P < 0.05$) among sites. Respiration rates in Lookout Creek and the McKenzie River are nearly an order of magnitude higher than in the two smaller streams.

Particle size and respiration rate are positively correlated ($P < 0.01$) only in Mack Creek and the McKenzie River (Fig. 7). In general, respiration rate by particle size does not show a consistent pattern for all streams but, rather, reflects biological conditioning associated with each unique stream segment and changes occurring in the composition and origin of organic matter as it is transported downstream.

A significant correlation between respiration rate and sample weight for Mack Creek, and the nonsignificant relationship between particle size and respiration in Devils Club Creek and Lookout Creek, cast some doubt about application of the data. We believe the data are, nonetheless, sufficiently valid to approximate the magnitude of respiration by drifting particles. Total respiration by particles $>106\ \mu m$, 53–106 μm, and 0.45–53 μm has been estimated using particle size: respiration rate regressions and empirical data on organic matter concentrations (Table 7). In summer, total respiration by drifting POM ranges from 24 to 144 $\mu L\ O_2 \cdot m^{-3} \cdot h^{-1}$, while autumn estimates range from 11 to 44 $\mu L\ O_2 \cdot m^{-3} \cdot h^{-1}$. Highest rates occur, however, during winter when organic detritus concentrations are greatest (36–233 $\mu L\ O_2 \cdot m^{-3} \cdot h^{-1}$).

In most cases respiration rate decreases as particle size decreases but most oxygen consumption occurs in the 0.45–53-μm size fraction, accounting for 57–97% of total respiration (Table 7). This is a reflection of VPOM dominance of drifting POM. Particles $>106\ \mu m$ account for only 1.5–27% of the total respiration; a reflection of their relative paucity. This may present a strategy delemma to consumer species feeding on microbes. Larger particles with higher respiration rates are relatively rare, whereas smaller particles are more abundant but generally have fewer microbes per unit weight.

C:N — Devils Club Creek and, in general, Mack Creek export organic matter with higher C:N ratios than Lookout Creek or the McKenzie River (Table 8). C:N did not decrease below 17 for any particle size in Devils Club Creek while, for Mack Creek, it did so for only a few particle sizes in summer and for one size in autumn. In contrast, Lookout Creek and the McKenzie River transport particles during all seasons with C:N at, or below, 17 for most sizes <1 mm.

These results are somewhat deceiving since, for many of the low C:N ratios, the percentage carbon in the samples is also small (Table 8). Carbon percentages for most samples are at least 30% but may decline below this level for small particle sizes in Lookout Creek and McKenzie River; indicating low C:N ratios may partially result from defractile nitrogen normally unavailable to microbes or consumers.

Food quality — Organic material drifting downstream represents a one-way coupling of energy from upstream areas to downstream reaches (Webster 1975). Webster (1975) and Wallace et al. (1977) discuss the concept of "spiralling" where the greater the amount of material cycling within a stream, the more efficient the stream is in processing organic matter and nutrients. Spiralling may be envisioned as a process whereby material is retained, then released, retained again, released, etc. When little spiralling occurs the system is inefficient and much material is moved downstream without being utilized. Wallace et al. (1977) reviewed the role of filter feeders in this process but did not give detailed analysis of food quality that might affect invertebrate distribution and abundance and thus the efficiency of streams in retaining and processing organic matter. Food quality is obviously important in determining the degree of spiralling and, in turn, the effectiveness of the system in retaining and processing organic material.

Microalgae are considered to be good quality foods because of their protein and lipid content but small heavily shaded streams have poorly developed

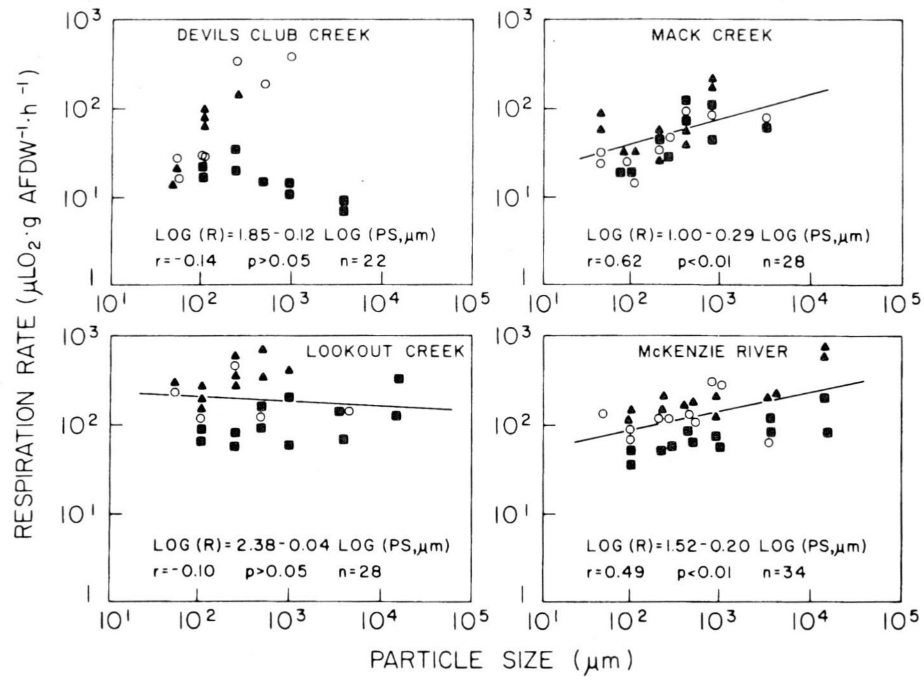

FIG. 7. Respiration is shown as a function of particle size for each stream: Winter (○), Spring (●), Summer (▲), Autumn (■).

TABLE 7. Total respiration of drifting particulate organic matter by particle size, site, and season.

Season	Particle size	Devils Club Creek $\mu L\ O_2 \cdot m^{-3} \cdot h^{-1}$	Devils Club Creek %	Mack Creek $\mu L\ O_2 \cdot m^{-3} \cdot h^{-1}$	Mack Creek %	Lookout Creek $\mu L\ O_2 \cdot m^{-3} \cdot h^{-1}$	Lookout Creek %	McKenzie River $\mu L\ O_2 \cdot m^{-3} \cdot h^{-1}$	McKenzie River %
Winter	>106 μm	10.6	29.9	2.0	5.4	5.3	2.3	7.2	8.0
	53–106 μm	2.6	7.3	4.3	11.7	1.5	0.6	6.8	7.5
	0.45–53 μm	22.3	62.8	30.4	82.9	225.8	97.1	76.0	84.4
	Total	35.5	100.0	36.7	100.0	232.6	100.0	89.0	99.9
Summer	>106 μm	4.0	16.5	2.0	5.6	6.9	4.8	16.5	18.8
	53–106 μm	4.5	18.3	6.0	16.7	8.8	6.1	7.0	8.0
	0.45–53 μm	15.9	65.2	28.2	77.8	128.7	89.1	64.1	73.2
	Total	24.4	100.0	36.2	100.1	144.4	100.0	87.6	100.0
Autumn	>106 μm	1.6	8.3	0.7	6.3	0.6	1.5	1.7	5.8
	53–106 μm	3.7	19.4	0.6	5.9	4.3	9.6	1.9	6.8
	0.45–53 μm	13.9	72.3	9.6	87.8	39.2	88.9	24.8	87.4
	Total	19.2	100.0	10.9	100.0	44.1	100.0	28.3	100.0

periphyton communities. In larger streams the canopy is open and the periphyton community well developed. During the normal course of growth and decay, periphyton sloughs a considerable amount of material to downstream reaches (Swanson and Backmann 1976; Liaw and MacCrimmon 1977; Naiman and Sibert 1978). In Lookout Creek and McKenzie River, during summer and autumn, chlorophyll accounts for a significant percentage of total drift (Fig. 6). Since only chlorophyll *a* was measured, detritus produced from decomposing periphyton was not detected. In autumn, however, as the periphyton community is waning, microalgae may be a considerable proportion of material transported in larger streams and, thus, may contribute to lower C:N ratios in downstream reaches.

Russell-Hunter (1970) indicated that a C:N of about 17 or less is necessary for efficient feeding and growth in most aquatic organisms. However, Ward and Cummins (1978) found the nitrogen content of detritus to be the least useful of the several parameters tested as growth-predictors for the collector *Paratendipes albimanus* (Chironomidae). They concluded that, de-

TABLE 8. C:N and percentage carbon of drifting particulate organic matter by size-group and season for each sampling location.

Season	Particle size	Devils Club Creek %C	Devils Club Creek C:N	Mack Creek %C	Mack Creek C:N	Lookout Creek %C	Lookout Creek C:N	McKenzie River %C	McKenzie River C:N
Winter	16 mm	—[a]	—[a]	—[a]	—[a]	—[a]	—[a]	32.8	18.5
	4 mm	—[a]	—[a]	—[a]	—[a]	43.8	15.8	43.3	19.9
	1 mm	—[a]	—[a]	45.6	25.3	17.9	17.4	33.7	13.0
	500 μm	34.6	32.9	44.3	28.5	16.7	12.7	36.7	14.4
	250 μm	35.4	36.1	41.7	27.8	17.0	12.6	37.7	15.2
	106 μm	36.1	34.0	36.8	33.1	17.2	12.5	38.3	19.0
	53 μm	36.2	35.8	30.4	24.9	—[a]	—[a]	36.7	20.6
Spring	16 mm	49.4	80.9	51.5	24.3	—[a]	—[a]	43.1	23.7
	4 mm	46.8	30.6	48.1	23.9	43.0	18.1	50.2	23.5
	1 mm	45.2	27.9	47.7	26.9	45.6	15.1	47.3	13.8
	500 μm	40.7	22.2	45.6	23.5	—[a]	—[a]	10.9	11.4
	250 μm	39.5	26.0	37.7	20.7	14.0	8.5	9.5	15.1
	106 μm	40.5	31.4	27.8	20.7	22.5	19.9	7.3	17.0
Summer	16 mm	—[a]	—[a]	—[a]	—[a]	—[a]	—[a]	49.4	38.0
	4 mm	—[a]	—[a]	—[a]	—[a]	46.0	17.4	52.5	14.2
	1 mm	—[a]	—[a]	46.1	19.4	39.5	8.3	46.6	15.2
	500 μm	—[a]	—[a]	45.5	15.4	33.3	9.7	36.8	14.3
	250 μm	41.7	34.9	41.3	20.7	31.7	10.5	34.5	14.5
	106 μm	41.8	22.5	36.4	18.0	30.2	9.6	28.6	17.3
	53 μm	36.5	19.9	32.0	14.8	19.3	10.7	15.7	12.1
Autumn	16 mm	—[a]	—[a]	48.8	31.9	—[a]	—[a]	47.5	22.0
	4 mm	—[a]	—[a]	51.0	37.2	51.5	30.6	45.9	22.7
	1 mm	—[a]	—[a]	51.3	36.7	23.6	21.5	10.8	15.2
	500 μm	—[a]	—[a]	46.6	30.1	5.4	12.3	4.0	15.0
	250 μm	40.0	28.8	5.9	9.9	11.9	14.2	40.4	37.8
	106 μm	41.6	28.9	8.9	19.4	16.6	17.1	37.1	30.4

[a]Either not enough material collected for analysis or the sample was lost.

spite a low C:N ratio, much of the nitrogen in downstream drift is of a refractory nature and not readily utilized by the associated microbes which constitute the primary nutritive source for the midge. With this in mind the importance of our C:N data must be interpreted with caution. To some extent the data support Ward and Cummins (1978) in that C:N is lower in Lookout Creek and the McKenzie River than in Devils Club Creek or Mack Creek, and some may be refractory nitrogen from areas far upstream. Also, the consumer invertebrate community is best developed in Mack Creek (Hawkins, Naiman, and Sedell unpublished data).

Nearly all drifting POM in Devils Club Creek and Mack Creek is derived from woody debris and leaves with inherently high C:N ratios. However, it is not known how much VPOM is of direct terrestrial input and, therefore, subjected to preprocessing in the terrestrial system. Wood and leaves sufficiently conditioned have low C:N ratios, and probably represent most material >106 μm. The low C:N ratio in material <106 μm partially results from periphyton, but could also be due to low amounts of carbon or high levels of refractory nitrogen. In any case, much of the material being transported in larger streams has the potential to be a good food source if the Russell-Hunter (1970) proposed C:N $\leq$ 17 range is correct.

Ward and Cummins (1978) found a good correlation between invertebrate growth and detritus respiration and ATP, respiration being used as an index of microbial activity on particles and ATP as an estimate of microbial biomass. Respiration rates on drifting organic particles are the same magnitude as organic particles in the substrate (Naiman and Sedell unpublished data), but do not correspond to the general relationships found by Hargrave (1972) for benthic detritus. In our measurements particle size and respiration rates are either positively correlated or there is no correlation (Fig. 7); for sediments an inverse relationship has been found (Hargrave 1972; Odum and de la Cruz 1967; Fenchel 1970). Hargrave (1972) related this negative relationship for sediments to surface area available for microbial colonization. This logical conclusion, however, does not hold for drifting organic particles. Bacteria on transported particles may produce growth regulating substances (Burkholder 1963), detritus may become more and more refractory as particles are decomposed and reduced in size, or bacteria could be physically removed by turbulence. The low respiration rates would support any of these postulates. Hargrave (1972) found rates for a wide variety of sediments to range from 0.1 to 10 mg $O_2 \cdot g$ $AFDW^{-1} \cdot h^{-1}$. In our experiments most rates ranged from 0.03 to 0.52 mg $O_2 \cdot g$ $AFDW^{-1} \cdot h^{-1}$; clearly at the low extreme. Whatever the cause, bacterial respiration on drifting organic matter is not great but, perhaps, the Gilson respirometer is not a good simulator for drifting particles. However, given the fact that respiration rates are higher on corresponding particle sizes in Lookout Creek and the McKenzie River than in the lower order streams, it can be concluded that drifting particles have a greater microbial activity in downstream reaches and, therefore, that the presumed food quality is better.

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