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Benthic organic matter as a function of stream order in Oregon

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With 4 figures and 6 tables in the text

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Abstract

The quantity, size composition and presumed food quality of organic detritus is compared in four coniferous forest streams of different order in the Cascade Mountains of Oregon, U.S.A. The amount of detritus is greatest in small headwater streams, and decreases as stream order increases. Over 90 % of detritus in all streams is woody debris; however, there is also a considerable quantity of fine particulate organic matter (FPOM: 0.45 μm to 1 mm) in small streams. Relative to the headwaters, downstream reaches have less coarse particulate organic matter (CPOM: > 1 mm) and FPOM. The CPOM : FPOM ratio appears to increase from 1st to 3rd-5th order streams, and decreases thereafter. The standing crop of benthic detritus and annual load of drifting particulate organic matter are used to evaluate the resistance and resilience of each stream order to perturbation. The results indicate that the pathway for attaining asymptotic ecosystem stability changes from one of resistance to resilience as stream order increases. Presumed food quality of the benthic detritus, as judged by the carbon-to-nitrogen (C : N) ratio, chlorophyll *a* associated with detritus, and respiration rate, is poor for CPOM and shows no trend by stream order. Presumed food quality of FPOM is somewhat better since, in larger streams, more chlorophyll is associated with the detritus and the highest respiration rates are associated with smaller particles.

Introduction

The importance of organic detritus to most ecosystems is well documented (Darnell, 1967; Odum, 1969; and Reichle et al., 1975) but only a few studies have been concerned with quantifying or characterizing the food quality and size composition of benthic organic detritus. In fact, until recently, no conceptual framework existed upon which the abundance and occurrence of various size fractions of detritus in streams and rivers of different orders could be placed (Cummins, 1975, 1977; Anderson et al., 1978).

Nelson & Scott (1962), Minshall (1967), Fisher & Likens (1973), and Cummins (1974) have shown allochthonous inputs and detritus to be important in stream communities as an energy base, and microorganisms associated with organic detritus are often important components of animal diets (NEWELL, 1965; HARGRAVE, 1970; BRINKHURST et al., 1972; CALOW, 1975; DAVIES, 1975; BROWN & SIBERT, 1977; WARD & CUMMINS, 1979). Studies of the relationship between food quality and life history parameters of several macroinvertebrates have found better growth and survivorship with foods either high in nitrogen (IVERSEN, 1974; BÄRLOCHER & KENDRICH, 1974) or with rich microfloras (WARD & CUMMINS, 1979). However, there are no detailed studies over several stream orders of the food quality of benthic organic detritus.

CUMMINS (1975, 1977) has theorized on the amount of benthic organic detritus and the distribution of particle sizes in streams and rivers. His concept is that coarse particulate organic matter (CPOM: > 1 mm) should be more prevalent in small, heavily shaded, headwater streams and of progressively less importance as stream order increases and terrestrial influences are reduced. Conversely, fine particulate organic matter (FPOM: 0.45 μm to 1 mm) should increase in importance as stream order increases due to abiotic-biotic processing of organic inputs. Therefore, the CPOM: FPOM ratio would tend to decrease as streams increase in size, and *in situ* biological processes (i.e., primary production, export from upstream areas) become more important.

Data are presented in this article for four Oregon streams to test CUMMINS's concept. In addition, various size fractions of benthic organic detritus are examined for presumed food quality. Organic matter associated with the benthos is compared to that being transported (NAIMAN & SEDELL, 1979), and the distribution and abundance of benthic detritus is related to geomorphic features of the stream channel. Proposed pathways for ecosystem development of relative stability are discussed for the various stream orders using benthic detritus and its turnover rate as indices.

Study sites

All sampling sites are located in the heavily forested Cascade Mountains of western Oregon (NAIMAN & SEDELL, 1979). The Cascade Mountains are characterred by high gradient streams, a maritime climate, and distinct seasonal rainfall. Three of the sites [Devils Club Creek (1st order), Mack Creek (3rd order), and Lookout Creek (5th order)] are in the H. J. Andrews Experimental Forest while the fourth site, the McKenzie River (7th order), is adjacent to the experimental forest. All streams experience strong autumn freshets and low summer flows. Annual precipitation ranges from 225 cm at lower elevations to 350 cm on the highest ridges. Highest elevations are characterized by extensive snow pack during winter, while rain predominates at lower elevations (BERNSTEIN & ROTHACHER, 1959). The dominant forest vegetation is Douglas-fir *(Pseudotsuga menziesii)*. Red alder *(Alnus rubra)* grows adjacent to most lower elevation streams.

Autochthonous and allochthonous inputs vary widely in total amounts and composition for each study site (NAIMAN & SEDELL, unpublished). Each organic input has a different propensity for drifting and different processing rates depending upon chemical 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 °C to 18 °C, and similar water chemistry (NAIMAN & SEDELL, 1979). The McKenzie River, however, has a smaller temperature range varying from about 3 °C in winter to 12 °C in summer, and water chemistry slightly different from other sites with higher concentrations of phosphorus, lower concentrations of nitrogen, and slightly higher alkalinity. All sites, however, are distinctly different in stream flow and channel morphometry. A detailed description of all sites is given in NAIMAN & SEDELL (1979).

Materials and Methods

Benthic organic matter concentrations were estimated at each site with pumps that collected organic matter from a known substrate area into a nested series of sieves. This collection device consisted of a 6 cm diameter hose, operated by a SCUBA diver, connected to a diaphragm ("Guzzler 90") hand pump on shore. Large pieces were collected by hand. Material taken from a 0.11 m^2 quadrat was divided into size classes of > 16 mm, < 16—> 4 mm, < 4—> 1 mm, < 1 mm—> 500 μm, < 500—> 250 μm, < 250—> 106 μm, and < 106—> 53 μm. Organic matter between 0.45 and 53 μm was estimated by subsampling water which had passed through the 53 μm sieve and was collected in a 160 L barrel. Coarse particulate organic matter (CPOM) is defined as material > 1 mm diameter; fine particulate organic matter (FPOM) as < 1 mm and > 0.45 μm (BOLING et al., 1975). As defined by temperature and flow, samples were collected in winter (March), spring (May), summer (July) and autumn (October), 1976.

In Mack Creek, Lookout Creek, and the McKenzie River 10 to 12 samples usually were taken on a single day each season while, because of its small size, only four samples were taken in Devils Club Creek. Collections were weighted based on areal percentage of pools, riffles, and alcoves.

Large woody debris (bole wood: > 10 cm diameter) in stream channels was measured by mapping its distribution, estimating dry weight by the methods of FROELICH et al. (1976); ANDERSON et al. (1978) and LIEMKAEMPER (unpublished) and assuming it to be 90 % organic. In autumn, immediately after leaf fall, distribution and abundance of leaves were determined by transects. Ten to twenty 0.11 m^2 quadrats were sampled over a 200 m reach at each site.

To study presumed food quality a large sample of benthic detritus was collected from each site, divided into the eight size classes, picked for invertebrates, and used for respiration estimates, chlorophyll extraction, and carbon and nitrogen

(C : N) determinations. In this article we are defining "food quality" as the amount of detritus which will presumably induce the most growth in consumers (both microbes and invertebrates) per unit of intake. Chlorophyll $a \cdot g$ AFDW^{-1} of detritus was estimated, using a Beckman spectrophotometer, by extraction in 10 ml of 90 % acetone (STRICKLAND & PARSONS, 1972). After chlorophyll extraction the detritus was weighed and then ashed at 500 °C. All samples were corrected for phaeopigments. Respiration rates ($\mu l\ O_2 \cdot g$ AFDW$^{-1} \cdot hr^{-1}$)* were measured with a Gilson respirometer. Samples were run in triplicate for each size class, and four to six readings were made for each sample at ambient stream temperatures in the shade. Samples were then weighed and ashed. Total carbon and nitrogen were determined on separate subsamples with a Carlo Erba Elemental Analyzer fitted with a CSI 208 integrator. Samples were dried and divided into two portions; one was used for C : N analysis and the other ashed.

Bole wood is not considered in the food quality studies for two reasons: A) It has a low biological activity (ANDERSON et al., 1978) and, B) It was too difficult to sample as part of our general program. It is currently being studied in detail at these sites by other investigators.

Unit stream power in an indication of the ability of water to move particles and can be estimated from the equation: $\omega = \frac{\varrho Qs}{w}$ where, ω is power per unit width (kg-m $\cdot s^{-1}$), Q is discharge in $m^3 \cdot s^{-1}$, s is slope in percent, width (w) is in meters, and ϱ is the density of water (LEOPOLD et al., 1964). This is the rate of work by flowing water per unit width of stream. The amount of organic material associated with the benthos is strongly influenced by stream power. Discharge was estimated with fluorescent dyes and from gauging stations, depending upon the site. Gradients were taken from United States Geological Survey topographic maps, and channel width was measured directly.

Results

Total Concentrations

All sites have significant accumulations of large woody debris (Table 1). Devils Club Creek has the largest standing stock of detritus (~ 26,000 g AFDW $\cdot m^{-2}$), of which about 91 % is woody debris > 10 cm diameter. Mack Creek (~ 14,800 g AFDW $\cdot m^{-2}$) and Lookout Creek (~ 6,000 g AFDW $\cdot m^{-2}$) have the next largest accumulations of benthic organic matter. However, bole wood still accounts for > 95 % of the total detritus in each stream. Although the McKenzie River does not have as much woody debris as the smaller streams, wood still accounts of > 90 % of the total standing crop of ~ 830 g AFDW $\cdot m^{-2}$.

When woody debris (> 10 cm) is removed from the total standing stock estimate it is apparent Devils Club Creek still has the greatest standing crop of smaller particles, followed closely by Mack Creek. Lookout Creek and the McKenzie River have low, and nearly identical concentrations of particles < 10 cm diameter.

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* AFDW = ash free dry weight.

Table 1. Mean seasonal standing crop of benthic organic matter (g AFDW · m^{-2})*. Large woody debris (> 10 cm) is estimated to be 23.75 kg · m^{-2} in Devils Club Creek, 14.25 kg · m^{-2} in Mack Creek, 5.75 kg · m^{-2} in Lookout Creek, and 0.75 kg · m^{-2} in the McKenzie River, with little season change (G. Lienkaemper, unpublished).

Site	Winter	Spring	Summer	Autumn	
				Total	Leaves
Devils Club Creek	26,992	25,370	26,046	24,790	74.3
Mack Creek	14,422	14,814	15,956	14,337	4.6
Lookout Creek	5,809	6,035	5,835	5,808	57.1
McKenzie River	875	826	802	828	8.2

* AFDW = ash free dry weight).

CPOM : FPOM Ratio

The ratio of coarse to fine organic matter shows that (1) coarse material is most abundant in all streams and that (2) there is no clear pattern in the ratio in response to stream order or season when all data are considered (Table 2). In Devils Club Creek the ratio ranges seasonally from 24 to 269, in Mack Creek the range is 24 to 327, and in Lookout Creek the values range from 68 to 171. Only the McKenzie River has consistently low ratios (12—22). The wider ranges measured for the Andrews Forest sites result from seasonal changes in FPOM due to transport downstream at high flows, the renewal rate from decomposition of larger particles, and probably inadequate sampling in winter at Devils Club Creek because of severe weather conditions and heavy snow pack. If the winter data from Devils Club Creek are ignored a clearer trend is evident. The ratio then

Table 2. CPOM : FPOM ratios for each study site by season.

Site	Winter	Spring	Summer	Autumn
Devils Club Creek	268.9	46.2	24.0	37.6
Mack Creek	326.7	79.1	23.8	280.1
Lookout Creek	171.1	67.8	139.4	169.3
McKenzie River	12.1	21.9	19.9	14.6

increases going from a 1st order to 3rd-5th order streams, followed by a decline as stream size and power increase.

Size Composition

Woody debris > 10 cm diameter has been excluded from an analysis of percentage composition of stream detritus because of its relatively slow decomposition. Material < 10 cm diameter is more readily available to the biological community even though some pieces may take years to decompose.

There is a progressive decrease in the percentage of total organic matter contributed by CPOM < 10 cm as stream order increases, with the mean percentage ranging from 65.3 % in Devils Club Creek to 40.4 % in the McKenzie River (Table 3). Correspondingly, the relative abundance of the

Table 3. Percentage of benthic organic matter in these size groups by site and season in 1976.

Site	Season	Percentage of benthic organic matter[1]		
		> 1 mm	1 mm to 53 μm	53 to 0.45 μm
Devils Club Creek	Winter	96.9	3.1	-
	Spring	66.8	29.7	3.5
	Summer	59.4	26.2	19.2
	Autumn	38.2	37.6	24.1
	Mean	65.3	24.2	15.6
Mack Creek	Winter	74.2	25.8	-
	Spring	67.2	26.7	6.1
	Summer	62.3	32.4	5.3
	Autumn	41.9	47.0	11.1
	Mean	61.4	33.0	7.5
Lookout Creek	Winter	41.8	18.5	38.7
	Spring	69.2	29.7	1.1
	Summer	47.8	41.7	7.2
	Autumn	41.2	45.3	13.5
	Mean	50.0	33.8	15.1
McKenzie River	Winter	50.4	13.8	39.7
	Spring	52.9	43.4	4.0
	Summer	26.2	61.3	12.5
	Autumn	31.9	56.9	11.1
	Mean	40.4	43.7	16.8

[1] Does not include large woody debris > 10 cm diameter.

1 mm to 53 μm fraction increases as stream order increases. This fraction comprises only 24.2 % of total benthic organic matter in Devils Club Creek but 43.9 % in the McKenzie River. The 0.45 to 53 μm fraction (very fine particulate organic matter: VPOM) is not especially significant at any site although in Lookout Creek and the McKenzie River it makes up 38.7 and 39.7 % in winter. Normally, the percentage of VPOM remains nearly constant (range: 7.5 to 16.8 %), with no trends related to stream order.

Chlorophyll

Chlorophyll associated with detritus in Devils Club Creek and Mack Creek is mostly derived from Douglas-fir needles, huckleberry *(Vaccinum)* leaves, and maple *(Acer)* leaves (Fig. 1). There is little production by algae in these streams because of shading by the forest canopy. In Lookout Creek algae occur in quantities during summer and autumn, contributing up to 1.3 mg chlorophyll *a* · g $AFDW^{-1}$ of detritus for a size class. The McKenzie River has considerable amounts of algae, aquatic mosses, and terrestrial leaf chlorophyll associated with detritus (Fig. 1) and, in autumn, algae contribute up to 3.9 mg chlorophyll *a* · g $AFDW^{-1}$ for a size class.

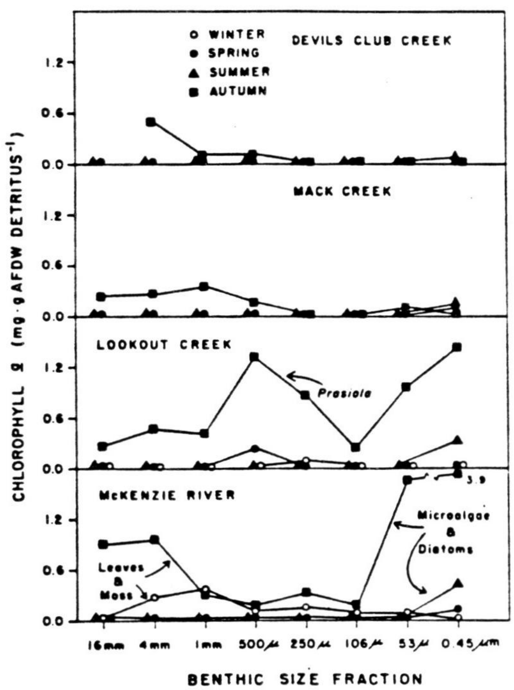

Fig. 1. Chlorophyll *a* associated with detritus is shown as a function of particle size for each site and season.

C : N Ratio

In Devils Club Creek the amount of carbon to nitrogen is high for all size fractions (Table 4). Other sites have high C : N ratios for CPOM; FPOM C : N ratios are generally ≤ 20. Devils Club Creek is dominated

Table 4. Carbon to nitrogen ratio for benthic organic matter by particle size, site and season.

Season	Particle Size	Devils Club Creek		Mack Creek		Lookout Creek		McKenzie River	
		%C	C:N	%C	C:N	%C	C:N	%C	C:N
WINTER	>16 mm	49.5	73.9	49.4	23.3	51.7	42.6	43.1	38.8
	4 mm	50.6	32.6	52.0	17.1	49.1	29.0	48.8	25.3
	1 mm	39.4	42.4	46.6	16.8	42.7	17.0	40.5	17.0
	500 μm	35.1	33.4	44.7	20.0	15.5	9.5	23.4	13.2
	250 μm	25.3	27.5	30.6	18.5	4.2	10.0	11.4	15.6
	106 μm	29.9	26.7	24.4	25.4	3.8	16.6	5.4	24.6
	53 μm	9.4	16.3	10.6	13.7	2.9	9.5	6.4	9.4
	0.5 μm	16.2	13.2	19.0	10.5	3.8	3.0	7.4	5.7
SPRING	>16 mm	53.2	94.9	53.7	41.6	53.9	77.0	51.6	48.2
	4 mm	51.6	45.2	14.0	24.0	51.1	31.7	54.2	16.5
	1 mm	49.5	41.2	50.6	50.1	49.7	23.0	52.1	16.0
	500 μm	29.5	37.8	43.1	21.3	39.7	18.8	35.8	14.0
	250 μm	2.1	4.4	2.1	4.1	5.0	7.4	0.7	22.7
	106 μm	23.8	34.0	4.5	26.2	4.7	9.9	0.4	*
	53 μm	24.2	17.9	9.5	21.2	3.7	12.7	1.7	17.2
	0.5 μm	25.1	14.9	18.6	17.5	7.4	5.6	3.6	*
SUMMER	>16 mm	33.8	51.2	56.6	69.0	51.6	79.4	39.4	43.8
	4 mm	52.5	31.1	52.2	35.3	51.8	31.8	51.0	37.3
	1 mm	37.3	19.8	45.4	41.3	25.2	24.4	31.8	36.9
	500 μm	44.9	25.8	34.1	17.4	15.9	18.8	11.4	18.0
	250 μm	39.8	23.4	11.9	10.1	0.6	*	0.5	*
	106 μm	26.6	32.5	12.7	18.4	2.8	21.2	0.7	*
	53 μm	7.6	23.0	8.9	19.7	1.3	0.6	1.3	33.0
AUTUMN	>16 mm	51.6	78.2	52.3	130.6	53.3	77.3	51.0	34.2
	4 mm	54.3	50.3	53.3	31.5	50.2	31.0	48.3	25.6
	1 mm	52.4	55.2	49.7	43.2	32.1	27.0	42.3	25.8
	500 μm	38.0	44.2	30.0	21.1	26.2	19.0	30.5	19.7
	250 μm	16.5	27.9	22.1	17.8	14.4	18.0	5.8	17.1
	106 μm	11.7	30.8	17.1	21.2	9.5	14.2	0.2	0.2
	53 μm	14.9	30.4	20.1	20.1	8.0	12.8	2.5	16.4

* = No nitrogen detected.

by woody inputs with inherently high C : N ratios while other sites also receive inputs of FPOM from upstream areas and periphyton. These latter inputs have low C : N ratios due to either microbial conditioning or inherently high nitrogen levels (e.g. periphyton).

Respiration

In each stream, respiration by the microbial community associated with the benthic detritus decreases as particle size increases ($r = -0.47$ to -0.58, ANOVA, $p < 0.01$)*, with no significant seasonal (temperature) effects (Fig. 2). The respiration rate normally ranges between 10 and 1,000 $\mu l\ O_2 \cdot g\ AFDW^{-1} \cdot h^{-1}$, depending upon the particle size, and is statistically similar among streams.

However, the metabolic rates observed in these experiments are strongly influenced by the sample weight used to make the metabolic measurements (Fig. 3). As sample weight increases the respiration rate decreases ($r = -0.62$ to -0.75, ANOVA, $p < 0.01$), without any significant seasonal differences. This may possibly be due to overloading the respiration vessels, although in nearly all cases < 0.8 g AFDW was used, the experi-

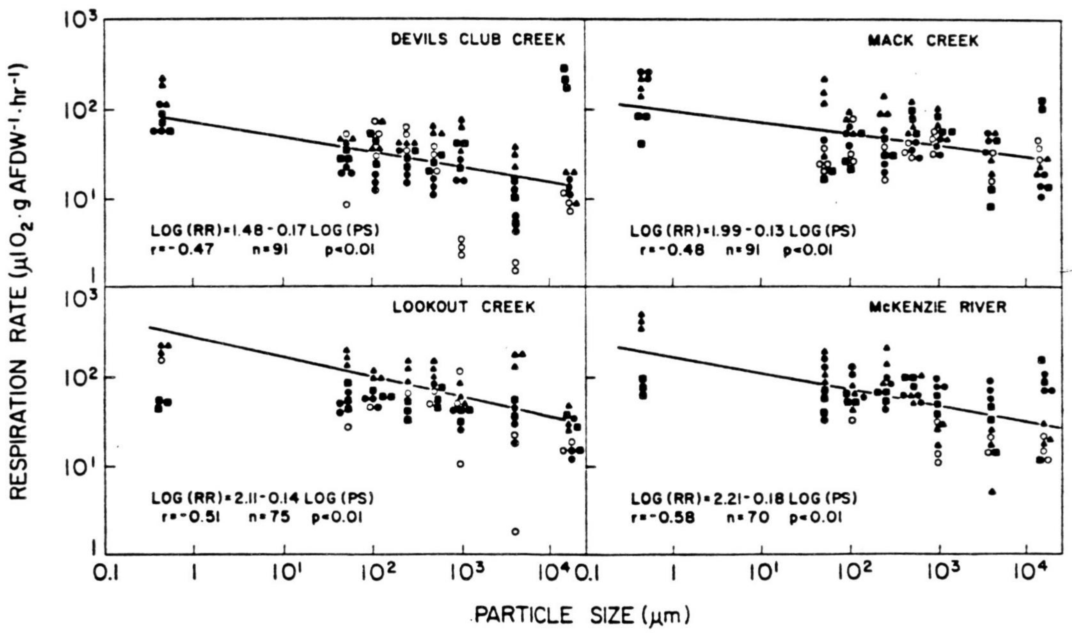

Fig. 2. Respiration rate is shown as a function of detritus particle size for each stream. (○) winter, (●) spring, (▲) summer, (■) autumn.

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* ANOVA = analysis of variance.

ments lasted only four to six hours, and no general decrease in respiration rate was noted over time.

Although the Gilson respiration procedure calls for equal sample weight per vessel it is often difficult to collect sufficient quantities of the smaller sized particles or small, representative amounts of the larger parti-

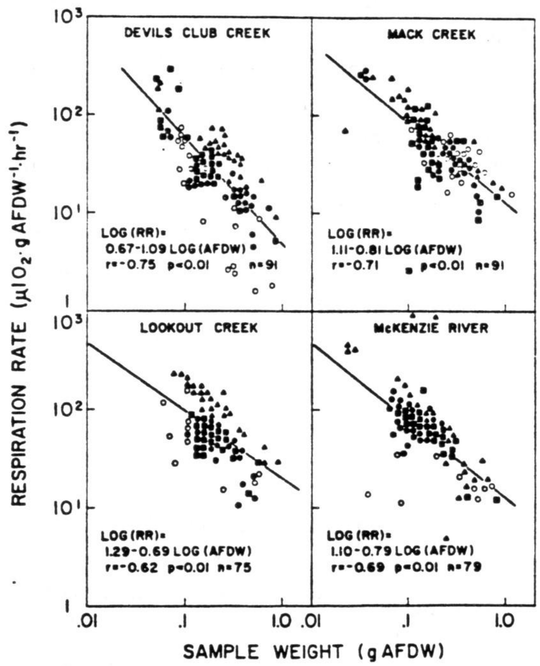

Fig. 3. Respiration rate is plotted as a function of sample weight used in the determinations. Symbols are: (○) winter, (●) spring, (▲), summer, (■) autumn.

Table 5. Respiration by benthic detritus and the ratio of CPOM to FPOM respiration by site and season in 1976.

Season	Devils Club Creek		Mack Creek		Lookout Creek		McKenzie River	
	Respiration[1]	CPOM:FPOM[2]	Respiration	CPOM:FPOM	Respiration	CPOM:FPOM	Respiration	CPOM:FPOM
Winter	4,956	5.73	4,465	3.67	4.999	0.06	2,086	5.53
Spring	8,905	0.47	12,816	1.21	6,373	0.89	4,535	1.94
Summer	88,665	0.27	33,067	2.31	9,155	1.99	6,292	0.04
Autumn	34,838	1.67	2,312	1.48	905	0.62	4,025	1.19

[1] Respiration ($\mu l\ O_2 \cdot m^{-2} \cdot hr^{-1}$).
[2] CPOM < 10 cm diameter.

cles. There are significant correlations between sample weight and particle size ($r = 0.56$ to 0.68, ANOVA, $p < 0.01$) for all sites because of these sampling difficulties. We feel, therefore, that further limited uses of the data are justified in light of these possible problems.

Respiration per unit area by all particle sizes < 10 cm can be calculated using respiration rate — particle size regressions for each season, in conjunction with the mean standing crop of detritus by particle size for that season (Table 5). Respiration at all sites is low in winter, rises slightly in spring, peaks during summer, and for all sites except Devils Club Creek, is low again in autumn. The proportion of respiration contributed by CPOM < 10 cm also changes seasonally. Most metabolism is associated with CPOM < 10 cm in Devils Club Creek, Mack Creek, and the McKenzie River in winter (Table 5). During winter in Lookout Creek most respiration is associated with FPOM. By summer in Devils Club Creek and the McKenzie River most of the metabolism has shifted to FPOM. In Mack Creek the ratio remains similar throughout the year, while in Lookout Creek most respiration is accomplished by CPOM < 10 cm in summer.

Discussion

Standing Crops

Cummins (1975, 1977) predicts a decrease in the CPOM : FPOM ratio as streams increase in size. This trend is not generally evident in Table 2, indicating the concept needs to be revised. In very small streams such as Devils Club Creek, efficient retention structures trap and hold a considerable amount of FPOM. These small streams can be envisioned as boundaries between terrestrial and aquatic ecosystems and, as a rule, are extremely efficient in retaining and processing organic inputs (Fisher & Likens, 1973; Naiman, 1976; Webster, 1977). When stream size increases by one or two orders, as for Mack Creek, hydraulic power is sufficient to overcome some retention structures to transport fine particles, but is insufficient during normal runoff events to move woody debris. Hence, there may be a slight increase in the CPOM : FPOM ratio going from 1st to 3rd or even 5th order streams. Larger streams (e.g. McKenzie River) have enough power during freshets to transport CPOM out of the normal channel. In this situation FPOM is rapidly renewed from upstream areas, whereas CPOM accumulates over a period of years, accounting for the relative abundance of FPOM in the substrate.

Variations in the total amount of benthic organic matter among sites is primarily due to accumulation of woody debris (> 10 cm) and FPOM from its decomposition. However, there are no apparent seasonal trends in total amount of benthic organic matter when bole wood is excluded. This seems somewhat unusual since autumn is a time of significant leaf fall and standing crops would be expected to increase substantially. Transects taken over a 200 m reach of stream bottom after leave abscission show most leaves to be in interstitial spaces between cobbles and, in most cases, leaf accumulations are small compared to the total amount of detritus in these streams (Table 1).

The particle size distribution (by weight) of benthic organic matter is definitely skewed toward larger particles in small streams, even with large woody debris removed (Table 3). Well over half of the detritus in Devils Club Creek and Mack Creek is CPOM < 10 cm; in Lookout Creek it is about half CPOM and, in the McKenzie River, CPOM is slightly less than one-half of the standing crop. Conversely, the percentage of FPOM dominates in downstream sections.

The amount of benthic detritus in streams, and its distribution, is a function of input rates, abiotic and biotic processing rates, stream power, retention structures, and channel morphometry. The proportion remaining on the substrate, transported downstream, or going into anaerobic storage (buried in the sediments) will be determined by physical processes such as the discharge regime and channel morphology. To move particles, stream power must be sufficient to overcome retention structures trapping organic material (e.g. woody debris, interstitial spaces, chemical binding, and animal communities). Channel morphometry affects both stream power and retention structures by superimposing spatial variability on the system, creating erosional and depositional zones. Examples of depositional areas are alcoves and eddies at the bend of a river which cause a decrease in stream power, or substrates with large cobble where considerable amounts of detritus are trapped in interstitial spaces as flow is reduced.

Power is largely determined by discharge in the high gradient streams of the Cascade Mountains. Thus, low discharge streams such as Devils Club Creek and Mack Creek have lower power despite relatively steep slopes (NAIMAN & SEDELL, 1979). Unit stream power (i.e. scaled for width) is also low. Additionally, those streams have efficient retention structures holding large amounts of organic material. Lookout Creek and the McKenzie River have relatively high power, few retention structures, and lower standing crops of detritus. Their unit power is large because of relatively narrow widths.

Small particles are easily moved by water and difficult to trap (NAIMAN & SEDELL, 1979); this is reflected in the standing crop of VPOM which normally comprises $< 20\%$ of the average annual total standing crop of organic detritus (Table 3). Most VPOM is in suspended transport with over 70% of drifting detritus being VPOM for all sites and seasons (NAIMAN & SEDELL, 1979). In Fig. 4 the particle size distribution of benthic

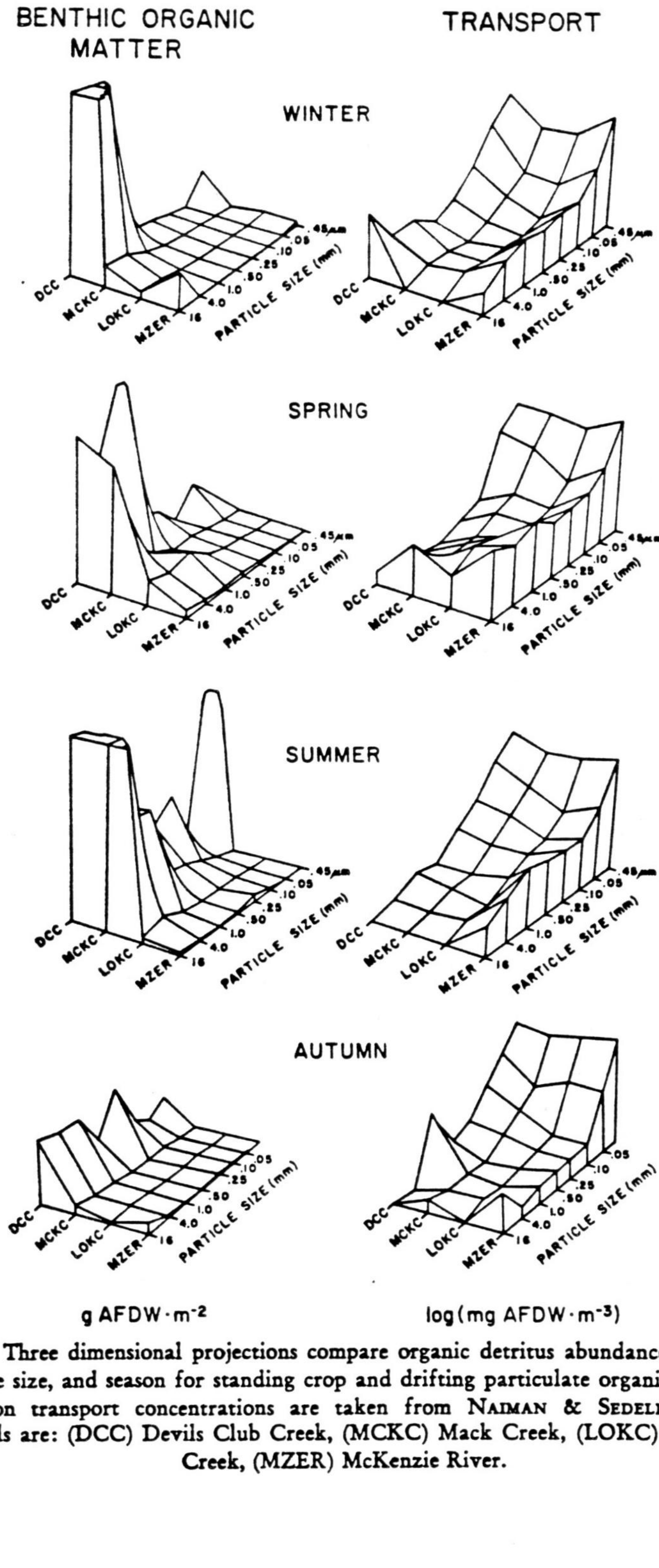

Fig. 4. Three dimensional projections compare organic detritus abundance by site, particle size, and season for standing crop and drifting particulate organic matter. Data on transport concentrations are taken from NAIMAN & SEDELL (1979). Symbols are: (DCC) Devils Club Creek, (MCKC) Mack Creek, (LOKC) Lookout Creek, (MZER) McKenzie River.

detritus is compared with organic material being transported. The mean particle size of drifting detritus ranges from 3 to 12 μm (NAIMAN & SEDELL, 1979), while the mean particle size (by weight) of benthic detritus is probably $> 500\ \mu m$, with the exact value depending on the total amount of woody debris. When retention structures are removed or overloaded with debris, as during some logging operations, it becomes easier for the stream to move particles. This can result in a dramatic decrease in the standing crop of fine detritus as evidenced in an experimentally clearcut watershed (WS-10) in the Andrews Experimental Forest (TRISKA, per. comm.). Material in disturbed stream reaches become part of the transported organic matter, as well as contributing to the standing crop in downstream reaches. This can be envisioned as follows: As stream power $\rightarrow \infty$, or retention structures $\rightarrow 0$, all material would be transported. When power $\rightarrow 0$, or retention structures $\rightarrow \infty$, all organic matter would be in the substrate. The relationship between power and retention structures determines the relative proportions of size classes present, and amounts being transported or in the substrate.

Resistance and resilience of Oregon streams

Two inverse concepts of ecosystem stability were developed by WEBSTER et al. (1975). Resistance is the ability of an ecosystem to resist displacement from equilibrium and results from the accumulated structure of the ecosystem; it is related to large storage of biomass or detritus, long turnover times, and large amounts of recycling. Resilience is the ability of an ecosystem to return to a reference state (equilibrium) once it is displaced; it reflects dissipative forces inherent in the ecosystem and rapid turnover and recycling rates.

MARGALEF (1960, 1963) considered small headwater streams to be immature ecosystems because they are supposedly unstable, being strongly influenced by abiotic factors and normally having a small biomass. Small streams draining forested watersheds, however, are detritus-based systems (FISHER & LIKENS, 1973). ODUM (1963, 1969) suggested that a detritus base is characteristic of relative maturity in ecosystems as it tends to buffer the system against disturbances. In small streams, detritus partially substitutes for living biomass by maintaining a degree or organizational integrity in the face of strong abiotic influences, such as current. In terms of the stream ecosystem, allochthonous litter lends stability (resistance and resilience to changes), and provides food to consumers without imposing a direct energy drain on the system (FISHER & LIKENS, 1973). Community stability is an important factor influencing the realization of maximum productivity in lotic environments (NELSON & SCOTT, 1962). Therefore, the stream segments studied can be considered stable based on detritus standing crops and organic input rates. In Devils Club Creek asymptotic stability results from large amounts of woody detritus imported from the adjacent forest, while in the McKenzie River stability results from inputs from upstream areas and autotrophic production.

Assuming that detritus standing crop and its relative turnover time are adequate measures of relative resistance and resilience we have determined Devils Club Creek to be the most resistant to change and the McKenzie River the least (Table 6). Devils Club Creek has the largest standing crop and the slowest relative turnover time. In contrast, the McKenzie River, because of its low standing crop and fast turnover, is the most resilient. Mack Creek and Lookout Creek are intermediate. It appears that the pathways for attaining asymptotic stability change very quickly as stream size increases. Small streams are more resistant to perturbations (large standing crop of detritus, long turnover) while larger streams are more resilient (large organic inputs, short turnover time); two opposing phenomena.

It is apparent then that entire stream networks cannot be classed as either resistant or resilient but, rather, streams with different abiotic-biotic characteristics will have different proportional combinations to achieve relative stability. Headwater streams in forested regions of the northwestern United States are dominated by woody inputs accumulated over decades. The pathway for attaining relative stability by these streams will be different than headwater streams dominated by annual leaf fall that does not accrue, or desert and high alpine streams with little allochthonous input.

Table 6. Mean annual discharge, annual transport load, mean annual standing crop of organic matter and annual turnover rate of benthic organic detritus.

Stream	Mean Annual Discharge[1] ($m^3 \cdot yr^{-1}$)	Annual Unit Transport Load[1,2] ($g\ AFDW \cdot m^{-1}\ yr^{-1}$)	Mean Annual Standing Crop ($g\ AFDW \cdot m^{-2}$)	Annual Turnover Rate[3] ($m \cdot yr^{-1}$)
Devils Club Creek	5.4×10^5	8.7×10^5	2.6×10^4	3.4×10^1
Mack Creek	2.9×10^7	5.7×10^6	1.5×10^4	3.8×10^2
Lookout Creek	1.2×10^8	5.8×10^6	5.9×10^3	9.8×10^2
McKenzie River	2.4×10^9	4.4×10^7	8.3×10^2	5.3×10^4

[1] Estimated from NAIMAN & SEDELL (1979).

[2] Estimated annual load of transported particulate organic matter divided by the stream width.

[3] Calculated by dividing annual unit transport load by the mean annual standing crop of benthic organic matter. This is a maximal estimate since respiration is not included.

Each stream segment will move toward relative stability, with the pathway depending upon the character of abiotic factors and organic inputs. The faunal community in each stream will reflect the physical resistance and resilience imparted to the system by geomorphic features, hydraulic regime, detritus, and organic input rates.

Food Quality

The quantity of organic detritus available as potential food is greater in upstream reaches but the quality of food items is apparently greater in downstream areas. Also, smaller particles are of a relatively higher quality than larger particles based on respiration rates and associated chlorophyll. The amount of detritus tells little about potential food quality since it is often not detritus that is the assimilated food item but microbes, nitrogen and algae associated with detritus (Cummins, 1974). The amount of chlorophyll *a*, the C : N ratio, and respiration rate are more reliable determinants of quality.

Algae associated with detritus is considered by us to be a potentially good food item becauese of its lipid and protein content. Few algae are associated with detritus in Devils Club Creek or Mack Creek because of shading by the forest canopy; however, in Lookout Creek and the McKenzie River a significant amount of algae are found in summer and autumn (Fig. 2). Assuming a carbon to chlorophyll *a* ratio of 120 (Gregory, 1979) and AFDW to be 50 % carbon, it is estimated that particle sizes between 0.45 and 106 μm in these two streams contain 0.1 to 28.5 % living algal carbon in summer and autumn.

The C : N ratio for particles $< 500\ \mu$m is usually low for all streams except Devils Club Creek (Table 4). This indicates that small particles in downstream reaches are relatively richer in nitrogen than larger particles, or any particles in first order streams. The utility of this ratio, however, has been questioned by Ward & Cummins (1979) who found poor correlations between the C : N ratio and growth in the detrivore *Paratendipes albimanus* (Chironomidae). C : N ratios are difficult to interpret since natural stream detritus probably contains refractory nitrogen compounds which are included in the C : N ratios but are minimally available to consumers. Our data may partially support the contention of Ward & Cummins since much of the reduction in the C : N ratio is caused by a disappearance of carbon, while the percentage of nitrogen changed only slightly (Table 4).

Ward & Cummins (1979) found the best correlations between growth rates and the respiration rate of microbes on detritus particles and ATP content. In Cascade streams no significant difference in respiration rate-particle size regression between sites or by season was obtained. Respiration rate did, however, vary inversely to particle size as found by HARGRAVE (1972) for a variety of situations. Highest metabolism is associated with the smallest particles. HARGRAVE (1972) reports respiration rates normally range from 0.1 to 10 mg $O_2 \cdot g$ $AFDW^{-1} \cdot hr^{-1}$. In our study all values were clustered around 0.1 mg $O_2 \cdot g$ $AFDW^{-1} \cdot hr^{-1}$, clearly at the lower extreme found by HARGRAVE. Low water temperatures for most of the year and low nutrients levels may be a partial explanation. Nevertheless, it appears that on an annual basis, much of the detritus may not be well conditioned in any stream, but smaller particles have higher microbial populations than larger particles per unit weight.

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Zusammenfassung

Quantität, Größen-Zusammensetzung und vermutliche Nahrungsqualität von organischem Detritus werden in 4 Nadelwald-Fließgewässern verschiedener Ordnung in den Cascade Mountains von Oregon, USA, verglichen. Die Detritusmenge ist am größten in kleinen Oberlauf-Bächen und nimmt mit steigender Gewässerordnung ab. Über 90 % des Detritus in allen 4 Gewässern bestehen aus Holzbruchstücken, doch befindet sich auch eine beträchtliche Menge feiner partikulärer organischer Substanz (0,45 μm bis 1 mm) in den kleinen Bächen. Im Vergleich zu den Oberläufen (Quellbächen) haben die stromabwärtsgelegenen Regionen weniger grobe (> 1 mm) und feine organische Substanz. Das Grob- zu Fein-Verhältnis scheint von Gewässern 1. bis zur 3. oder 5. Ordnung anzusteigen und bei noch höheren Ordnungsziffern wieder abzunehmen. Die vorhandene Menge an benthischem Detritus und die Jahresfracht der driftenden partikulären organischen Substanz werden zur Bestimmung der Resistenz und der Elastizität (resilience) der Fließgewässer verschiedener Ordnung bei Störungen benutzt. Die Ergebnisse zeigen, daß der Weg zur Erreichung asymptotischer Ökosystem-Stabilität mit steigender Gewässerordnung von Resistenz zu Elastizität wechselt. Die vermutliche Nahrungsqualität des benthischen Detritus, beurteilt nach dem C : N-Verhältnis, nach der im Detritus enthaltenen Chlorophyll-a-Menge und nach der Respirationsintensität, ist gering für die grobe partikuläre organische Substanz und zeigt keinen Trend in bezug auf die Gewässerordnung. Etwas besser ist die Nahrungsqualität der feinen partikulären organischen Substanz, da in größeren Fließgewässern mehr Chlorophyll im Detritus enthalten ist und die höchsten Respirationsraten bei den kleineren Partikeln auftreten.

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