Relationships Between Metabolic Parameters and Stream Order in Oregon

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NAIMAN, R. J., AND J. R. SEDELL. 1980. Relationships between metabolic parameters and stream order in Oregon. Can. J. Fish. Aquat. Sci. 37: 834–847.

The light regime, standing stock of chlorophyll, and five metabolic parameters were measured seasonally at four Oregon stream sites; Devils Club Creek (1st order), Mack Creek (3rd order), Lookout Creek (5th order), and the McKenzie River (7th order). Periphyton from pools and riffles, aquatic moss (*Fontinalis*), fine particulate organic matter (FPOM: $0.5\ \mu m$–1 cm), and coarse particulate organic matter (CPOM: >1 cm) were examined separately for gross production (GP), net community production (NCP), diel respiration (R_{24}), net daily metabolism (NDM), and the production to respiration (P:R) ratio. Total autotrophic production was found to increase in a downstream direction where more light is available; however, the efficiency of light utilization is greatest in heavily shaded Mack Creek. Detrital metabolism, per unit weight, is similar in all streams for each metabolic parameter. The standing stock of detritus though, is highest in headwater streams, decreasing as streams become larger. Therefore, the relative contribution of the detritus community to total metabolism decreases downstream. Mosses occur in significant quantities only in the McKenzie River and have an areal community respiration rate about twice that of periphyton; other metabolic parameters are nearly equal in this case. On an areal basis periphyton metabolism is much greater than detrital metabolism and, as a consequence, total stream metabolism and the P:R ratio increase downstream.

Gross production rates measured for these sites are some of the lowest recorded (0.1–1.0 $g\ O_2 \cdot m^{-2} \cdot d^{-1}$). These rates are compared to those from other streams in the northwestern United States and western Canada, and the importance of photosynthesis to stream systems is demonstrated. The decomposition rate of the detrital standing stock is estimated to be 0.0029–0.0057$\% \cdot m^{-2} \cdot d^{-1}$ and the turnover time is calculated to be 48–93 yr for particles <10 cm in diameter.

Key words: streams, rivers, metabolism, primary production, detritus, photosynthesis, chlorophyll, respiration, light, Oregon

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Le régime lumineux, la biomasse de chlorophylle et cinq paramètres métaboliques ont été déterminés saisonnièrement à des sites de quatre cours d'eau de l'Orégon : ruisseau Devils Club (1er ordre), ruisseau Mack (3^{e} ordre), ruisseau Lookout (5^{e} ordre) et rivière McKenzie (7^{e} ordre). Nous avons examiné séparément le périphyton des fosses et des radiers, la mousse aquatique (*Fontinalis*), le matériel organique particulaire fin (FPOM : 0,5 μm–1 cm) et le matériel organique particulaire grossier (CPOM : >1 cm) afin d'en déterminer la production brute (GP), la production communautaire nette (NCP), la respiration nycthémérale (R_{24}), le métabolisme quotidien net (NDM) et le rapport production : respiration (P : R). On constate que la production autotrophe totale augmente vers l'aval où il y a plus de lumière; cependant, l'efficacité d'utilisation de la lumière est maximale dans le ruisseau Mack, fortement ombragé. Le métabolisme détritique, par unité de poids, est semblable dans tous les cours d'eau pour chaque paramètre métabolique. Cependant, la biomasse détritique est maximale dans les cours d'eau de tête et diminue à mesure que les cours d'eau grossissent. La contribution relative de la communauté détritique au métabolisme total diminue donc vers l'aval. Les mousses ne se trouvent en quantités importantes que dans la rivière McKenzie et ont un taux respiratoire communautaire par superficie environ deux fois plus élevé que celui du périphyton; les autres paramètres métaboliques sont dans ce cas à peu près égaux. Sur base de superficie, le métabolisme du périphyton est de beaucoup supérieur au métabolisme détritique et, comme conséquence, le métabolisme total du cours d'eau et le rapport P:R augmentent vers l'aval.

Les taux de production brute mesurés à ces sites sont les plus bas qu'on ait enregistrés

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Printed in Canada (J5781)
Imprimé au Canada (J5781)

(0,1 à 1,0 g $O_2 \cdot m^{-2} \cdot jour^{-1}$). Nous comparons ces taux à ceux d'autres cours d'eau du nord-ouest des États-Unis et de l'ouest du Canada et démontrons l'importance de la photosynthèse dans les réseaux fluviaux. On estime à 0,0029–0,0057% $\cdot m^{-2} \cdot jour^{-1}$ le taux de décomposition de la biomasse détritique et calcule que la période de renouvellement est de 48 à 93 ans pour des particules de diamètres < 10 cm.

Received September 14, 1979
Accepted January 25, 1980

Reçu le 14 septembre 1979
Accepté le 25 janvier 1980

RELATIVE proportions of total metabolism by autotrophic and heterotrophic components of streams is largely a function of the physical dimensions of the stream channel, which affects the light regime, nature of allochthonous inputs, and discharge patterns. Normally, small headwater streams in forested areas are heavily shaded, and have considerable detritus associated with the substrate (Naiman and Sedell 1979, 1980). As stream size increases the forest canopy opens, allowing more light to reach the water surface, and correspondingly higher discharge rates transport detritus out of the stream channel and downstream. Extensive periphyton and macrophyte communities develop in these medium-sized streams, direct detrital inputs from the forest are less, and the metabolic importance of detritus to total stream metabolism is usually reduced over that in the headwaters. Further downstream, as the forest canopy opens completely and the river becomes deep and turbid, the autotrophic component is largely restricted to a phytoplankton community, while the mineralization of fine detritus being transported now plays a larger metabolic role (Cummins 1975, 1977; Vannote et al. 1980).

This generalization has been developed from studies of specific stream sites but has never been adequately tested in a single river system. Previous studies of community metabolism have been restricted to single reaches, usually only primary production or total metabolism have been measured, and because of the ease of sampling, these studies have been largely conducted on small streams. There is only one study of periphyton over several stream orders (Seyfer and Wihlm 1977), and few comprehensive studies of larger streams and rivers (Wetzel 1975; Schmidt 1976; Fisher 1977). Only Odum (1957), Teal (1957), Tilly (1968), Fisher and Likens (1973), Naiman (1976), and Fisher (1977) have attempted to isolate the various components of total metabolism in stream ecosystems, usually concentrating on springs and low-order streams.

In this study we examined gross production (GP), net community production (NCP), diel respiration (R_{24}), net daily metabolism (NDM), and the production to respiration ratio (P:R) of autotrophic and detrital components of stream segments ranging from a small headwater stream to a moderately large river. These data are used to test the hypothesis that the P:R ratio is <1 in small streams where there is considerable detritus and reduced light levels, the ratio increases to >1 in midorder reaches where the detrital standing crop is reduced and the forest canopy is partially open; and the ratio decreases to <1 as water depth increases, the river becomes turbid, and metabolism associated with drifting fine detritus increases in relative importance. Our measurements and observations were made on the McKenzie River system in western Oregon, USA.

Study Area

The McKenzie River originates in Oregon's Cascade Mountains. It is characterized by high gradient stream channels, a maritime climate, and considerable seasonal rainfall. All streams in the Pacific Northwest experience autumn and spring freshets and low summer flows; annual precipitation ranges from 225 cm at lower elevations to about 350 cm on ridges. High elevations have extensive snow pack during winter; rain predominates at lower elevations (Berntsen and Rothacher 1959). Dominant forest vegetation is Douglas fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*). Red alder (*Alnus rubra*) is associated with lower elevation streams. Three of the four study sites (Devils Club Creek, Mack Creek, and Lookout Creek) are within the H. J. Andrews Experimental Forest about 70 km east of Eugene, Oregon, and one (McKenzie River) is adjacent to the forest (Fig. 1). The dynamics of drifting organic matter (Sedell et al. 1978; Naiman and Sedell 1979) and benthic detritus (Naiman and Sedell 1980) have been previously reported for these streams.

Devils Club Creek is a first-order stream (Strahler 1957) heavily shaded by forest, and with a poorly developed autotrophic community (Table 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*), devilsclub (*Oplopanas horridum*), maple (*Acer macrophyllum* and *Acer circinatum*), and Douglas fir needles (Naiman and Sedell 1979, 1980). Devils Club Creek discharges directly into Mack Creek.

Mack Creek is one of three major channels draining the Andrews Forest. The morphology of this third-order stream is characterized by a stairstep of gouged pools, free fall zones, and turbulent water around large boulders (Table 1). Substrate ranges from large boulders to sand but is mostly loose cobble (Sedell et al. 1975). Woody debris is prevalent but less concentrated than in Devils Club Creek (Anderson et al. 1978; Naiman and Sedell 1980). The forest canopy is slightly open and patches of light reach the stream at midday. Wind-borne debris, lateral movement from steep side

FIG. 1. A, Devils Club Creek; B, Mack Creek; C, Lookout Creek; D, McKenzie River. All study sites are located in the Cascade Mountains about 70 km east of Eugene, Oregon.

slopes, and downstream transport of organic matter from tributaries are the primary organic inputs. Mack Creek is a major tributary of Lookout Creek.

Lookout Creek (5th order), receiving runoff from most of the Andrews Forest, has shallow riffles interspersed with small pools; the substrate is large cobbles and bedrock. There is relatively little woody debris in the stream, the canopy is open, and most sunlight reaches the periphyton community. Primary production by diatoms (*Melosira*), filamentous algae, and stream lettuce (*Prasiola*), as well as transport from upland areas, are the major organic inputs (Naiman and Sedell 1979, 1980). Allochthonous inputs from maple leaves and conifer needles are important primarily only in late summer and autumn. Lookout Creek discharges into Blue River, a tributary of the McKenzie River.

The McKenzie River is a major seventh-order stream draining the western Cascade Mountains. Morphologically, it is 85% riffle-runs with a few alcoves or pools. Substrate is cemented cobble and large boulders; large amounts of woody debris have not accumulated (Table 1; Naiman and Sedell 1980). Alder and Douglas fir along stream margins contribute some organic matter but most inputs are from upstream transport, periphyton production, and aquatic macrophytes. A zone of aquatic mosses (*Fontinalis* sp.) extends 5 m from both banks.

Organic inputs vary widely in amount and composition for each study site (Naiman and Sedell 1979, 1980). All Andrews Forest sites have similar temperature regimes with winter lows of about 1°C and summer maxima of about 15 to 18°C, and similar water chemistry (Table 1; Naiman and Sedell 1979). The McKenzie River has a narrower annual temperature range varying from about 3°C in winter to 12°C in summer, and a slightly different water chemistry with

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TABLE 1. Physical characterization of the Oregon study locations.

Parameter	Devils Club Creek	Mack Creek	Lookout Creek	McKenzie River
Stream order	1	3	5	7
Watershed area (km^2)	0.2	6.0	60.5	1024.0
Mean width (m)	0.6	3.0	12.0	40.0
Mean depth (m)	0.05	0.22	0.90	1.60
Benthic organic matter (g AFDW$\cdot$m^{-2})	28 800	14 882	5 872	833
Forest canopy development	Closed	Mostly closed	Mostly open	Open
Mean annual discharge (L$\cdot$s^{-1})	1.7	92	377	75 300
Benthic substrate	Detritus	Boulders–cobbles	Cobble	Cobble
Temperature range (°C)	1–15	1–16	1–18	3–12
Total chlorophyll (mg Chl $a\cdot$m^{-2})	19–48	36–95	18–96	31–90
Nutrient range (μg$\cdot$L^{-1})				
NO_3-N	0.3–23.5	3.4–76.0	0–43.2	0–4.2
PO_4-P	3.9–12.8	5.8–12.4	7.3–15.4	28.2–49.6
Alkalinity range (mmol$\cdot$L^{-1})	0.063–0.137	0.056–0.132	0.013–0.131	0.167–0.244

higher concentrations of phosphorus, lower concentrations of nitrogen, and slightly higher alkalinity. All sites are quite different in stream flow, channel geometry, and basin morphometry (Table 1), but all have the exceedingly clear water typical of high montane salmonid streams.

Methods and Materials

GENERAL APPROACH

The major metabolic components of each stream were measured separately because a natural section of substrate could not be accommodated by the metabolic chambers. The autotrophic component was either mosses or periphyton on rocks; periphyton was further identified depending as to whether the rocks were from a riffle or pool. The heterotrophic component consists of animals and microbes associated with detritus. Animal metabolism is usually a small percentage of the total community metabolism (Naiman 1976) and was not measured in this study. Detritus was separated according to size; woody debris (CPOM) consisted of cones, bark, leaves, needles, and wood >1 cm in diameter. For this study only, fine particulate organic matter (FPOM) was considered to be smaller debris, generally <1 cm in diameter. Total stream metabolism was estimated for each site by combining all metabolic components on an areal basis.

In these streams large woody debris >10 cm in diameter (bole wood) is the major detrital component, comprising over 90% of the detrital standing crop. Nearly all of this material is in the form of trees up to 1 m in diameter (Naiman and Sedell 1980). Metabolism associated with this material was not measured because (1) much of it is in the stream channel but not under water, (2) it could not be realistically sampled and placed in the chambers, (3) and, although it is an important structural component of streams, it has a low biological activity, decomposing over very long time periods (Anderson et al. 1978).

TECHNIQUES AND PROCEDURES

Sampling was in March (winter), May (spring), July (summer) and October (autumn), 1976. Winter data for Devils Club Creek and Mack Creek are minimal because of heavy snow accumulations and severe weather that restricted access.

Periphyton, moss, and detritus were collected, placed in separate sealed recirculating Plexiglas metabolic chambers (volume: 14 L), and oxygen changes monitored with YSI oxygen meters connected to a strip chart recorder (Bott et al. 1978). All chambers were placed in the stream from which the samples had been collected, except for Devils Club Creek. In this instance the chambers were placed about 30 m away in Mack Creek because Devils Club Creek was too small to hold them. It is felt that no serious errors resulted from this since Devils Club Creek and Mack Creek have a similar water chemistry and temperature regime (Naiman and Sedell 1979), and a similar light regime. Metabolic parameters were measured by the diel oxygen method (Bott et al. 1978) using the following equations:

1) Gross primary production (GP) = net community primary production plus community respiration during photoperiod.
2) Net community primary production (NCP) = GP − R_{pp}.
3) Community respiration (R) = total respiration during photoperiod (pp) or diel period (24).
4) Net daily metabolism (NDM) = GP − R_{24}. The net change caused by community metabolism over a diel period.
5) P:R ratio = GP ÷ R_{24}.

Four chambers were run simultaneously for various periods ranging up to 96 h at each location. During winter and spring samples in the chambers were changed after 4 d, with each diel period considered to be a separate data point. In summer and autumn samples were replaced after 2 d with each day used as a separate metabolic measurement. Normally, all chambers were flushed every 4–8 h to avoid oxygen, nutrient, and CO_2 depletion stress. Metabolism of microbes on the Plexiglas was <5% ($n = 4$) of samples placed in the chambers, even after 4 d of continuous submergence. Incident radiation at the water surface was measured continuously with a LiCor model 185 quantum radiometer.

After each experiment the chamber contents were placed in containers, frozen, and returned to the laboratory. The

TABLE 2. Daily light regime ($\mu E \times 10^5 \cdot m^{-2} \cdot d^{-1}$) at the water surface for each sampling location during the metabolic experiments.

	Devils Club Creek		Mack Creek		Lookout Creek		McKenzie River	
Season	$\bar{x} \pm$ SE	n	$\bar{x} \pm$ SE	n	$\bar{x} \pm$ SE	n	$\bar{x} \pm$ SE	n
Winter	4.4	1	5.1	1	75.0±9.2	4	70.4±17.7	4
Spring	24.7±8.7	4	33.3±6.9	5	177.2±39.7	4	101.5±20.7	4
Summer	10.1±0.5	4	11.1±1.5	4	165.0±25.7	6	67.3±10.4	6
Autumn	2.7±1.0	3	2.7±0.8	4	98.1±9.5	4	130.0±28.9	4

ash-free dry weight (AFDW) of material in each chamber was determined by drying to a constant weight at 60°C and ashing a subsample at 550°C for 4 h. Prior to drying, chlorophyll was extracted by immersion in 1 L of 100% acetone for 24 h. Water associated with the samples reduced the final acetone concentration to about 90%. Chlorophyll *a* was calculated using the equation of Lorenzen (1967). Surface area of rocks was measured by wrapping each rock with aluminum foil, weighing the foil, and converting to area using the weight of foil per unit area. Of the total rock area, about 50% is photosynthetically available and 25% is available when viewed as a horizontal plane from above the stream (T. D. Bott, personal communication; Gregory 1979). Therefore, multiplying total rock area by 0.25 gave the photosynthetic area in m^2 of stream bottom.

It was not possible to measure the metabolism of the intact benthic community because of the wide range of particle sizes encountered, turbulence of the water, and spatial segregation of the metabolic components. Because of this results for each metabolically active component were combined to estimate total metabolism in the following manner. In chambers with only detritus, metabolism was measured in $g\ O_2 \cdot g\ AFDW^{-1}$ of detritus per day. This value was combined with measurements of the seasonal standing stock of detritus <10 cm in diameter (Naiman and Sedell 1980) to estimate total detrital metabolism in $g\ O_2 \cdot m^{-2} \cdot d^{-1}$. This was added to metabolic measurements of periphyton on rocks to estimate total community metabolism. In the McKenzie River an estimate of total metabolism is complicated because of the moss (*Fontinalis*) component. Moss occurs over ~5% of the total area; therefore total metabolism was prorated as: 0.05 (moss metabolism) + 0.95 (periphyton metabolism) + detritus metabolism.

Concomitant with the oxygen measurements an effort was made to measure photosynthetic and respiratory quotients by the method of Talling (1973). Each time chambers were flushed, water samples were collected in stoppered containers and the alkalinity determined by Gran titration with 0.1 N HCl and a Coleman 80 pH meter. The results obtained were not considered reliable. Photosynthetic quotients ranged from −14.5 to 17.5, respiratory quotients ranged from −7.0 to 2.6, with nearly all values far from the predicted quotients of 1.25 and 0.85 for protein metabolism, respectively. Our attempts to measure the PQ and RQ will not be presented here because of these facts, although the problems we encountered are worthy of notation.

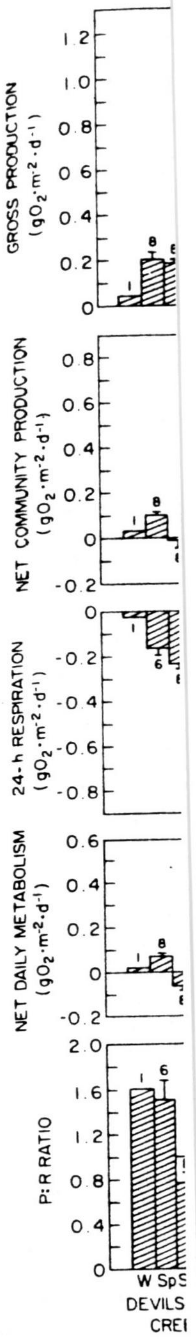
Results and Discussion

LIGHT

Light regime — There is a significant difference in the light regime among streams (ANOVA, $P < 0.05$). Little sunlight reaches the stream surface in Devils Club Creek and Mack Creek (Table 2). Highest light levels for both streams occur during spring before understory shrubs and small trees (huckleberry, devilsclub, and maple) develop their seasonal foliage. Lookout Creek and the McKenzie River are wide enough to have a relatively open canopy. The difference in the light regime between these latter two streams is caused mainly by the directional orientation of the sites and by spatial placement of the chambers and light meter. The channel of Lookout Creek is oriented east–west; the McKenzie River channel is oriented north–south. Also, the McKenzie River, because of its powerful current, necessitated that chambers be placed near to shore and, as a consequence, some shading by riparian vegetation did occur during summer and autumn that was not characteristic of most of the stream channel. In addition, for all streams, the daily light regime is quite variable because of weather common in this geographical region.

THE AUTOTROPHIC COMPONENT

Periphyton metabolism — There is a steady increase in gross production, net community production, and diel respiration by periphyton as stream size increases from 1st-order Devils Club Creek to 5th-order Lookout Creek. Lookout Creek and the McKenzie River have nearly identical metabolic rates (Fig. 2). Seasonal estimates of gross production range from 0.1 g $O_2 \cdot m^{-2} \cdot d^{-1}$ in Devils Club Creek to about 0.9 g $O_2 \cdot m^{-2} \cdot d^{-1}$ in the McKenzie River. Net community production ranges from zero to about 0.6 g $O_2 \cdot m^{-2} \cdot d^{-1}$, while diel respiration varies from −0.1 g $O_2 \cdot m^{-2} \cdot d^{-1}$ in the Devils Club Creek to almost −0.7 g $O_2 \cdot m^{-2} \cdot d^{-1}$ in the McKenzie River. Metabolism is generally lowest in winter and autumn for all sites except the McKenzie River where the lowest metabolic rate occurs during spring snowmelt.



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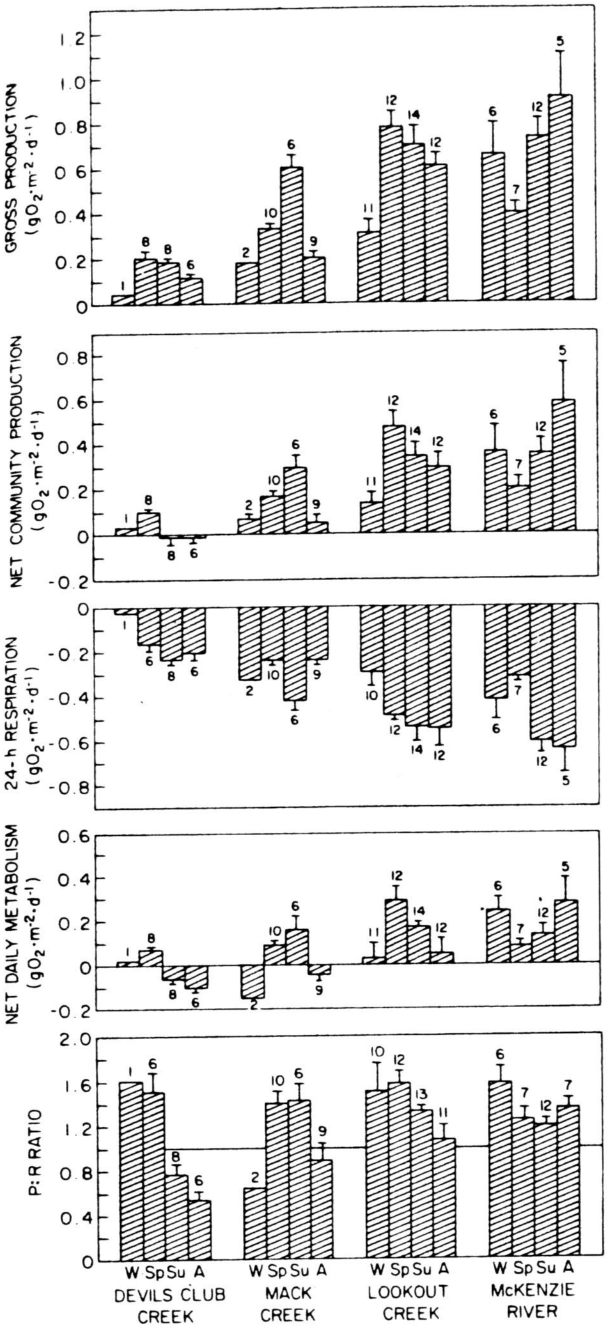

FIG. 2. Mean, SE, and sample size of measurements of gross production, net community production, diel respiration, and the P:R ratio of the periphyton community in each stream. Symbols are winter (W), spring (Sp), summer (Su), and autumn (A).

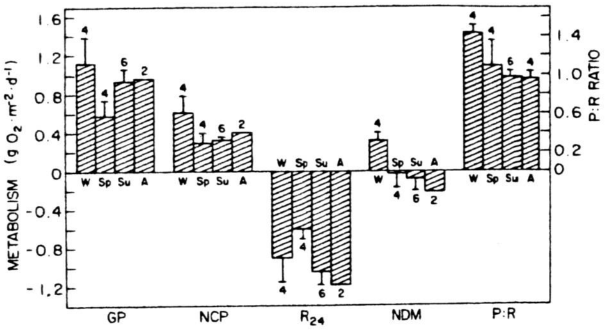

FIG. 3. Metabolism by moss in the McKenzie River compared by season. Mean, SE, and sample size are shown. Symbols are the same as in the previous figure.

Net daily metabolism is lowest in Devils Club Creek (0.1 g $O_2 \cdot m^{-2} \cdot d^{-1}$) and often negative (Fig. 2); at other sites it is generally positive, ranging up to 0.3 g $O_2 \cdot m^{-2} \cdot d^{-1}$, and of nearly equal magnitude for each stream. In this case there are no definite seasonal trends; highest values are in winter and spring for the McKenzie River; spring and summer in Lookout Creek; winter, spring, and summer in Mack Creek; and spring for Devils Club Creek.

P:R ratios have only a slight trend by stream order; each stream has periphyton P:R ratios >1 for at least part, if not all of the year (Fig. 2). The P:R ratio in Devils Club Creek is >1 in spring; the winter period should be viewed with caution since only one sample was obtained. Mack Creek exhibits a P:R ratio during spring and summer that is equal to or greater than those measured for periphyton in Lookout Creek and the McKenzie River.

Moss metabolism — Gross production, net community production, and diel respiration remain nearly constant throughout the year for the *Fontinalis* dominated community in the McKenzie River, except for a slight decrease in the respiration rate and, consequently, gross production during the spring freshet (Fig. 3). Gross production ranges from 0.6 to 1.1 g $O_2 \cdot m^{-2} \cdot d^{-1}$; net community production ranges up to 0.6 g $O_2 \cdot m^{-2} \cdot d^{-1}$; and diel respiration ranges from about −0.6 to −1.2 g $O_2 \cdot m^{-2} \cdot d^{-1}$. Net daily metabolism is positive during the winter period and slightly negative at other times. However, standard errors for spring and summer estimates indicate accrual of organic matter is possible during these periods. The P:R ratio approximates unity throughout the year.

Chlorophyll — The standing stock of chlorophyll *a* in each stream is the same order of magnitude, ranging from 18 to 96 mg $Chl \cdot m^{-2}$, although Devils Club Creek is lowest for all seasons (Table 3). Surprisingly, heavily shaded Mack Creek has more chlorophyll at times than Lookout Creek or the McKenzie River. Our results are comparable to those reported by Lyford and Gregory (1975), who found concentrations ranging from 8 to 35 mg $Chl \cdot m^{-2}$ in Mack Creek and 8 to 45 mg $Chl \cdot m^{-2}$ in Lookout Creek over a 1.5-yr period. The amount of chlorophyll at these sites is comparable to that measured in other streams of the northwestern

TABLE 3. Mean seasonal concentration ($mg \cdot m^{-2}$) of chlorophyll *a*, and ratio of optical density at 665 μm before and after acidification, of rocks and detritus in each stream.

														McKenzie River						
		Devils Club Creek				Mack Creek				Lookout Creek				Periphyton				Mosses		
Season		n	$\bar{x} \pm$ SE	%	665/665a	n	$\bar{x} \pm$ SE	%	665/665a	n	$\bar{x} \pm$ SE	%	665/665a	n	$\bar{x} \pm$ SE	%	665/665a	n	$\bar{x} \pm$ SE	665/665a
Winter	Rocks	1	12.3	66.7	1.41	2	36.0	99.4	1.73	7	18.3±2.2	100.0	1.59	4	58.1±11.5	93.4	1.63	2	202.8	1.66
	Detritus	2	6.2	33.3	1.00	2	0.2	0.6	1.65	2	0.0	0	1.32	3	4.1±4.0	6.6	1.45			
	Total		18.6				36.2				18.3				62.2					
Spring	Rocks	2	18.8	88.7	1.58	3	49.5±5.2	91.2	1.66	3	59.7±5.6	97.5	1.75	2	31.1	99.7	1.61	1	28.9	1.12
	Detritus	2	2.4	11.3	1.43	1	4.8	8.8	1.53	1	1.5	2.5	2.29	1	0.1	0.3	1.51			
	Total		21.2				54.3				61.2				31.2					
Summer	Rocks	3	22.7±3.6	78.8	1.61	4	84.3±11.9	88.5	1.67	6	39.7±7.5	98.8	1.64	4	53.8±9.3	99.4	1.61	2	276.2	1.64
	Detritus	4	6.1±3.9	21.2	1.54	4	11.0±3.8	11.5	1.57	2	0.5	1.2	1.74	2	0.3	0.6	1.92			
	Total		28.8				95.3				40.2				54.1					
Autumn	Rocks	4	26.1±3.1	54.8	1.74	4[a]	61.9±13.6	95.8	1.67	6	96.0±11.9	99.7	1.66	4	89.1±11.9	99.6	1.62	2	441.2	1.65
	Detritus	4	21.5±17.1	45.2	1.36	3	2.7±2.0	4.2	1.61	2	0.3	0.3	1.55	2	0.4	0.4	1.63			
	Total		47.6				64.6				96.3				90.3					

[a] Excluding a measurement of 312.2 mg $Chl \cdot m^{-2}$ (665/665a = 3.15) from a chamber containing rocks covered with mosses.

United States and western Canada (Stockner and Shortreed 1976; Lane 1965; Cushing 1967).

The ratio of gross production to the standing stock of chlorophyll *a*, used here as an assimilation number, is markedly different between the lower- and higher-order streams (Table 4). In Devils Club Creek and Mack Creek, the seasonal ratio was generally between 3 and 8 while in Lookout Creek and the McKenzie River it ranged from 10 to 18. The ratios for the larger streams are similar to those found by McConnell and Sigler (1959) for a mountain river in Utah; the ratios for Devils Club Creek and Mack Creek are much lower. However, most of the assimilation numbers reported here are within the general range of 4.8 to 48.0 given by Odum et al. (1958) for whole communities.

Mean seasonal chlorophyll concentrations are significantly correlated with four of the five metabolic parameters (Table 5); only the P:R ratio does not have a significant correlation ($r = 0.08$). Best relationships are between gross production, net community production, and diel respiration. Why the P:R ratio does not have a significant correlation with chlorophyll is intriguing. Chlorophyll concentrations are roughly similar for all streams (Table 3) suggesting differences in metabolic rate are largely determined by light availability. Therefore, given a similar temperature regime, it appears standing stock of chlorophyll may determine the basic level of metabolism, while light strongly influences the active level of metabolism, as well as relative proportions involved in growth and respiration.

Efficiencies and correlations — It is evident that each stream, regardless of its size or light regime, has an active autotrophic community. Although the importance of the autotrophic community is relatively slight in Devils Club Creek, the P:R ratio often exceeds unity. Periphyton has more sites available for attachment in Mack Creek, and it is more important here, with some metabolic parameters nearly equal to those in Lookout Creek and the McKenzie River. These observations raise two questions: (1) Is the active level of periphyton metabolism a function of available light? (2) Are periphyton communities in shaded situations more efficient in their utilization of light? These questions can be partially answered by examining comparative efficiency of light utilization.

There is a significant difference in gross light efficiency between streams (ANOVA, $P < 0.05$) but not among season ($P > 0.05$) (Table 6). Gross efficiency of light utilization [(Gross production/g cal light) 100] in Devils Club Creek is normally about 1% but may be as high as 4% in autumn. In Mack Creek efficiency ranges seasonally from <1 to 5%, while efficiencies in Lookout Creek are about 0.5% and in the McKenzie River about 1%, suggesting that periphyton from shaded streams are more light efficient than periphyton from streams where the canopy is open. However, factors not studied here, such as herbivore grazing and scouring during freshets may be just as

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TABLE 4. Mean gross production (GP) and net daily metabolism (NDM) per milligram of chlorophyll *a* in the periphyton component, for each stream by season. Units are mg $O_2 \cdot$mg $Chl^{-1} \cdot d^{-1}$.

	Devils Club Creek		Mack Creek		Lookout Creek		McKenzie River	
Season	GP	NDM	GP	NDM	GP	NDM	GP	NDM
Winter	3.6	1.5	5.1	4.2	17.0	2.0	11.4	4.2
Spring	10.5	3.8	6.7	1.8	13.1	4.8	12.8	2.6
Summer	7.8	−2.8[a]	7.1	1.9	17.7	4.3	13.8	2.4
Autumn	4.1	−3.9[a]	3.2	−0.7[a]	6.4	0.5	10.3	3.1

[a] Negative value caused by a net loss of organic matter over the diel period.

TABLE 5. Correlations between mean seasonal chlorophyll *a* concentrations and mean seasonal metabolic parameters for the periphyton community in all streams. Metabolic parameter units are mg $O_2 \cdot m^{-2} \cdot d^{-1}$; chlorophyll is mg$\cdot m^{-2}$. $n = 16$; $*P < 0.05$; $**P < 0.01$.

Metabolic parameter	Correlation (r)	Equation
Gross production (GP)	0.77**	$\text{Log}_{10}(\text{GP}) = 0.81 + 1.07 \log_{10}(\text{chl})$
Net community production (NCP)	0.69**	$\text{NCP} = 4.78\,(\text{chl}) - 8.11$
Diel respiration (R_{24})	−0.73**	$R_{24} = -132.34 - 4.81\,(\text{chl})$
Net daily metabolism (NDM)	0.48*	$\text{NDM} = 2.13\,(\text{chl}) - 3.73$
P:R ratio	0.08	

important as light availability in determining standing stock of chlorophyll and the level of periphyton metabolism in natural streams (Tett et al. 1978).

Attempts to correlate available sunlight with the five metabolic parameters at a single site gave correlation coefficients (r) generally <0.4 and significant at $P = 0.05$ in only 7 of the 20 possible cases (five parameters in four streams). The narrow range of sunlight values recorded for any one stream, in combination with seasonal variability due to temperature, chlorophyll standing crop, and discharge regime appeared to be primary causes for these results. When data for all streams are combined, the relationship between light and metabolism becomes clearer (Table 7). For each metabolic parameter the relationship is highly significant ($P < 0.001$) but the correlation coefficients are not large and only 17 to 41% of the variation in the measured metabolism can be attributed to variations in the light regime. This indicates that other factors, such as current, scouring, chlorophyll, and temperature, are also important in determining periphyton metabolic rates. The relative proportion of production to respiration (P:R:), however, is more a function of light than chlorophyll. Chlorophyll is not significantly correlated with P:R ($r = 0.08$, Table 5), while the correlation with light is highly significant ($r = 0.41$, $P < 0.001$, Table 7).

TABLE 6. Calculated gross efficiency (%) of light utilization by periphyton.

	Devils Club Creek	Mack Creek	Lookout Creek	McKenzie River
Season	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE	$\bar{x} \pm$ SE
Winter	0.9	2.3	0.3±0.05	0.8±0.16
Spring	0.8±0.26	0.9±0.21	0.7±0.11	0.3±0.08
Summer	1.3±0.07	3.6±0.44	0.3±0.02	0.8±0.12
Autumn	4.2±1.41	4.9±0.72	0.4±0.04	1.0±0.53

When mean seasonal gross production is scaled to a unit of chlorophyll (assimilation number) and regressed against mean seasonal sunlight (e.g. using light data collected during the seasonal experiments) there is a highly significant relationship ($r = 0.87$, $P < 0.001$) (Fig. 4). Nearly 76% of the stream to stream variation in the assimilation number can be attributed to light and nearly all the differences in gross production are caused by the interaction of light and chlorophyll.

Autotrophic comparisons—Mack Creek can be characterized as having moderately delineated pools and riffles while in Lookout Creek they are well separated. The other sites are almost entirely riffles. Biological differences between pool and riffle habitats in terms of species, chlorophyll, and diversity are well known. Hynes (1972) and others (e.g. McIntire 1966) have demonstrated the effects of current speed on periphyton metabolic processes. In Mack Creek, depending upon the season, pool periphyton metabolism can be lesser or greater than riffle periphyton (Table 8). Pools here are small and, at high flows, essentially become riffles. On the other hand, in Lookout Creek pool periphyton metabolism is usually only 40–80% of that measured for riffle periphyton. However, for gross pro-

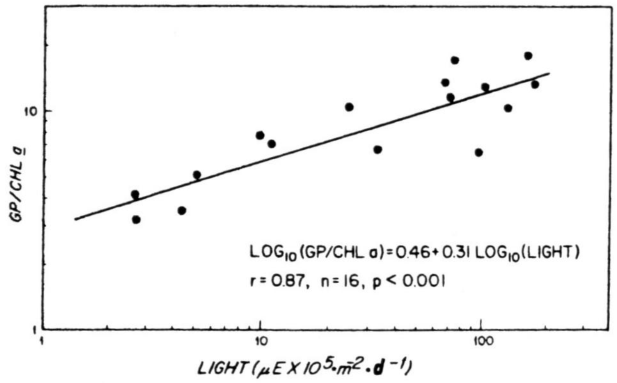

FIG. 4. The positive relationship between available sunlight and the assimilation number (GP/Chl *a*) using seasonal averages for each stream.

duction, there is a statistically significant difference between habitats only when spring and summer data are combined and compared to combined winter and autumn data *t*-test, $P < 0.05$). When all pool data are compared to all riffle data a significant difference is not present. It is interesting though, that in Lookout Creek the pool P:R ratio is equal to or greater than the riffle P:R ratio for three of the four seasons. In calculating the total periphyton metabolism of Lookout Creek the data were prorated by seasonal pool:riffle percentages; the other sites were not treated in this manner.

Mosses are a conspicuous component of the McKenzie River system but are thought to yield less material to higher trophic levels than periphyton primarily because of higher maintenance costs due to accrued biomass. *Fontinalis* is a perennial macrophyte with the biomass taking several years to accumulate. Compared to periphyton, gross production, net community production, and diel respiration by mosses are 17 to 83% greater (Fig. 5). However, most of the gross production of the moss community is due to its respiration. The result is that net daily metabolism by periphyton is about 550% greater than mosses and the P:R ratio is slightly higher for periphyton, suggesting that periphyton is the more significant of the two in directly determining overall river productivity.

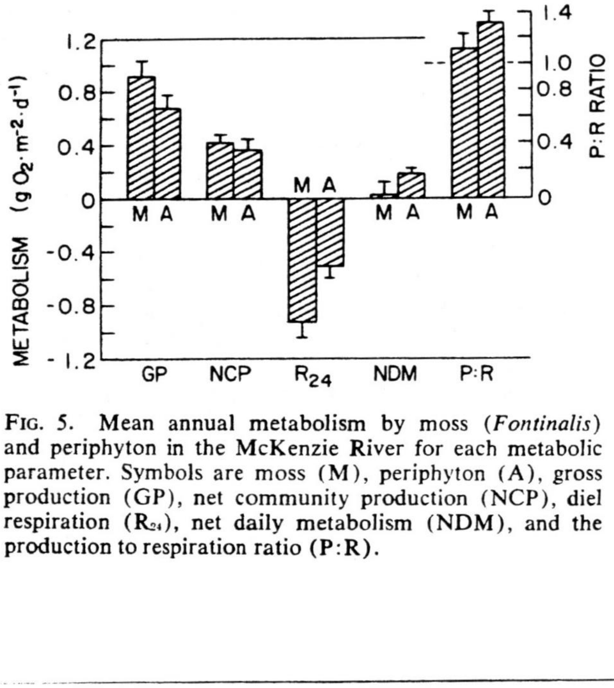

FIG. 5. Mean annual metabolism by moss (*Fontinalis*) and periphyton in the McKenzie River for each metabolic parameter. Symbols are moss (M), periphyton (A), gross production (GP), net community production (NCP), diel respiration (R_{24}), net daily metabolism (NDM), and the production to respiration ratio (P:R).

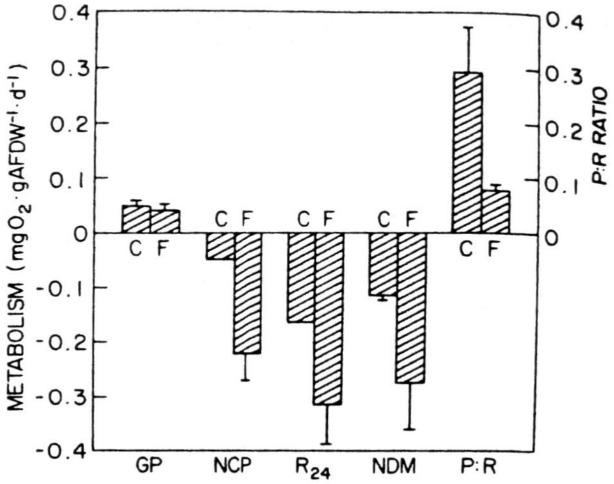

FIG. 6. Mean annual metabolism by coarse particulate organic matter (C) and fine particulate organic matter (F). Key to most symbols is given in Fig. 5; AFDW is ash-free dry weight.

THE DETRITUS COMPONENT

CPOM and FROM — Respiration rates are a function of particle size and, hence, surface area available for microbial colonization (Hargrave 1972; Naiman and Sedell 1980). These latter studies, restricted to particles less than about 1.6 cm in diameter, indicated respiration rates of benthic detritus are inversely proportional to particle size. However, the relationship between particle size and respiration rate of material being transported by the current is not clear (Naiman and Sedell 1979). To date, no one has examined metabolism by detritus particles greater than about 1.6 cm in diameter. On a weight basis CPOM comprises >90% of total detrital matter in each stream (Naiman and Sedell 1980); however, it would be expected from the studies of Hargrave (1972) and Naiman and Sedell that metabolic activity of CPOM would be considerably lower than FPOM.

In addition to microbes, there can be considerable microalgae associated with detritus (Table 4) (Anderson et al. 1978). This will vary from a few percent of the total stream chlorophyll (Lookout Creek and McKenzie River) to as much as 45% in Devils Club Creek. CPOM, because of its size, provides a relatively stable substrate for algal attachment and growth. Algae can also be attached to FPOM detritus particles but the stability of those particles is far less than for CPOM, and

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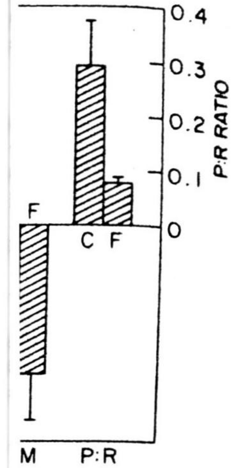

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TABLE 7. Equations relating metabolic parameters to surface sunlight for all streams and seasons combined. Sunlight units are microEinsteins ($\mu E \times 10^5$); metabolic units are mg $O_2 \cdot m^{-2} \cdot d^{-1}$.

Metabolic parameter	Sample size (*n*)	Equation	Correlation coefficient (*r*)	Significance
Gross production	129	$\text{Log}_{10}(\text{GP}) = 0.350 \log_{10}(\mu E) - 0.98$	0.64	$P < 0.001$
Net community production	127	$\text{Log}_{10}(\text{NCP}) = 0.073 \log_{10}(\mu E) - 0.03$	0.59	$P < 0.001$
Diel respiration	126	$\text{Log}_{10}(R_{24}) = 0.211 \log_{10}(\mu E) - 0.80$	0.50	$P < 0.001$
Net daily metabolism	126	$\text{NDM} = 0.130 \log_{10}(\mu E) - 0.11$	0.46	$P < 0.001$
P:R	127	$\text{Log}_{10}(\text{P:R}) = 0.135 \log_{10}(\mu E) - 0.16$	0.41	$P < 0.001$

TABLE 8. The ratio of metabolism by pool versus riffle periphyton for the five metabolic parameters measured in Mack Creek and Lookout Creek each season.

	Mack Creek							Lookout Creek						
Season	GP	NCP	R_{24}	NDM	P:R	Pool samples (*n*)	Riffle samples (*n*)	GP	NCP	R_{24}	NDM	P:R	Pool samples (*n*)	Riffle samples (*n*)
Winter	0.7	2.4	0.4	0.1	1.9	1	1	0.8	0.8	0.5	3.3	1.3	4	7
Spring	0.8	0.5	1.1	0.2	0.7	3	7	0.7	0.6	0.8	0.4	0.8	4	8
Summer	1.5	2.4	1.0	17.6	1.6	4	2	0.6	0.6	0.6	0.6	1.0	10	4
Autumn	1.9	72.0	0.9	−0.6[a]	2.2	3	6	1.0	1.0	0.8	−5.4[a]	1.3	6	6

[a] Negative value caused by a negative measurement for riffle periphyton.

the degree of shading from other particles is certainly greater. Depending upon the local situation photosynthesis by algae associated with detritus can be significant.

Gross production per unit of weight is nearly identical for both CPOM and FPOM (Fig. 6). However, net community production, diel respiration, and net daily metabolism of CPOM are only 23–53% of the FPOM metabolic rate. Conversely, the CPOM P:R ratio is nearly four times greater than FPOM. This is primarily due to more periphyton being associated with larger particles. These results indicate that CPOM and FPOM components of detrital metabolism must be treated separately in determining total stream metabolism.

Total detritus — Metabolism by the detrital community will either be a function of total standing crop at each site or influenced by stream to stream differences in metabolic activity per unit weight. There are no significant differences ($P > 0.05$) in metabolism per unit weight of detritus between streams and there are no seasonal trends; only detritus from Mack Creek in summer has a higher than normal metabolic rate but considerable variability is associated with those estimates (Fig. 7). This substantiates our earlier results using a Gilson respirometer with small particle sizes, that similar particle sizes have similar respiration rates, per unit of weight, between sites (Naiman and Sedell 1980). Differences of the total detrital community metabolism between sites are therefore due to differences in the standing stock of detritus.

Combining metabolism per unit weight of detritus (Fig. 7) with the mean seasonal standing crop of CPOM and FPOM (Naiman and Sedell 1980) gives an estimate of the metabolic activity of the total detritus standing crop (Fig. 8). Gross production of microbial communities on detrital substrates is the same for all streams each season. However, net community production, diel respiration, and net daily metabolism are highest in Devils Club Creek and Mack Creek where there are the largest standing stocks of detritus. All metabolic rates are negative in these streams, indicating a net degradation of organic matter. In some cases metabolic rates measured in Lookout Creek and the McKenzie River are slightly positive but, in all cases, are only a fraction of those measured in the two smaller streams. P:R ratios are generally <0.2 for detritus in Devils Club Creek and Mack Creek, rising to the 0.2–0.6 range in larger streams where more light is available for photosynthesis by associated microalgae.

If we assume all degradation of CPOM and FPOM is due to microbial activity and that all respiration is involved in the mineralization of particulate detritus, then respiration rates associated with CPOM and FPOM can be used to estimate the turnover time and decomposition rate of each detrital component. Using a factor of 2.75 to convert oxygen to carbon, given the fact that detritus is ~50% carbon, and using the standing crop estimates from Naiman and Sedell (1980), we calculate that for CPOM <10 cm in diameter in all streams the decomposition rate is $0.0029\% \cdot m^{-2} \cdot d^{-1}$ and the turnover time is ~93 yr. For FPOM the decompo-

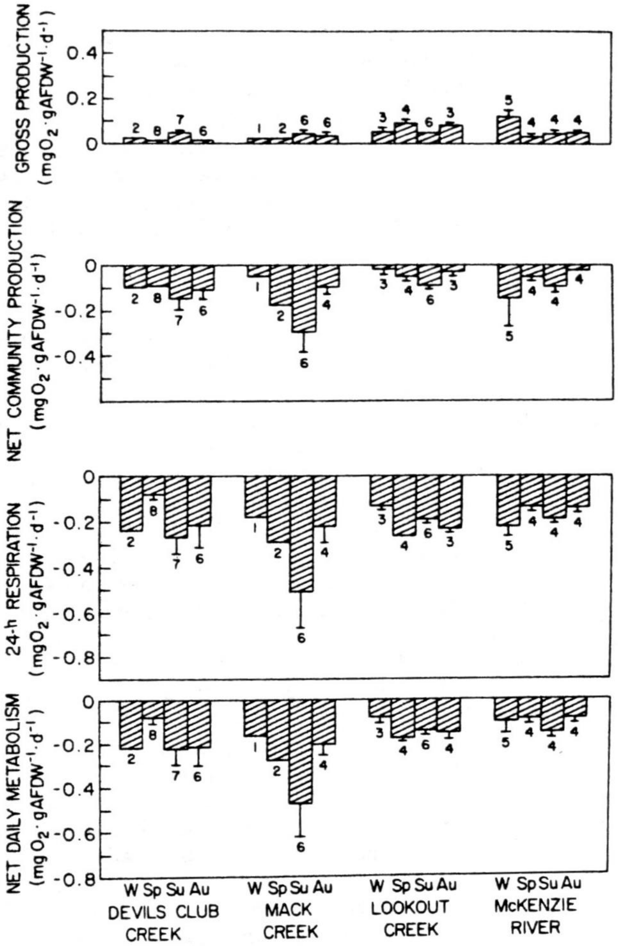


FIG. 7. Metabolism of detritus per unit of weight by site and season. Mean, SE, and sample size are given; symbols are described in previous figures.

sition rate is faster (0.0057% $\cdot m^{-2} \cdot d^{-1}$) and the turnover time is shorter (~48 yr). If these estimates are realistic, it can then be expected that CPOM >10 cm in diameter would take considerably longer to be decomposed by microbial action, possibly 200–300 yr.

The time required for wood to decompose in freshwater has been estimated on only a few occasions. For woody debris in the streams studied here, Anderson et al. (1978) gave a degradation time of 5–200 yr with limited data on respiration rates. They did clearly show, however, that the role of invertebrates in wood decomposition is minor, giving a conservative estimate of 1–1.7% $\cdot yr^{-1}$. Hodkinson (1975) predicted a 57-yr half-life for 7.5-cm-diameter logs of *Populus balsamifera* in a cold water beaver pond in Alberta, Canada, and Fisher and Likens (1973) give a turnover time of 4.2 yr for small wood in Bear Brook, New Hampshire. The role of physical abrasion in the wood decomposition has never been evaluated, but it may be an important aspect of the process, especially since the role of microbes and invertebrates appears to be minor.

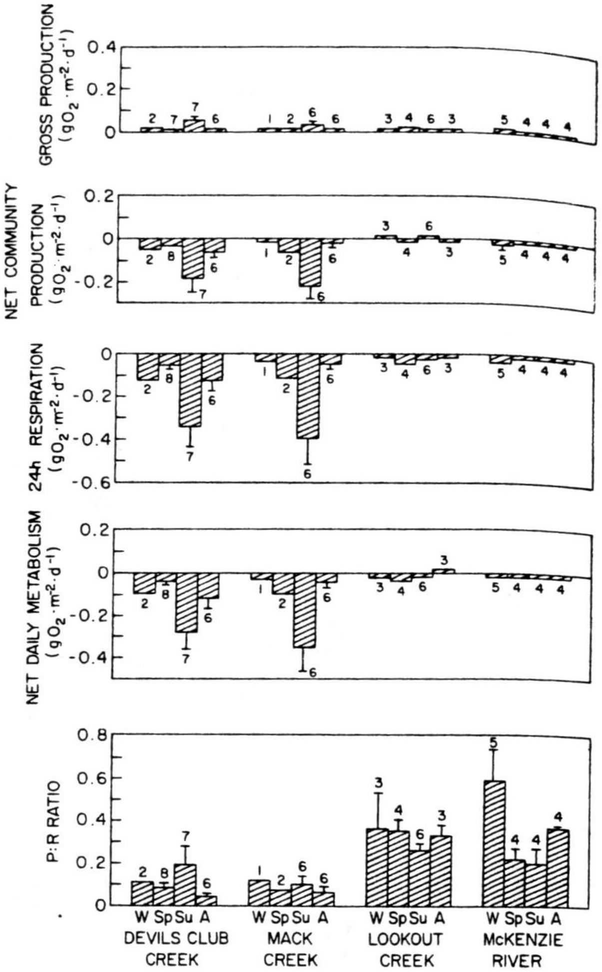
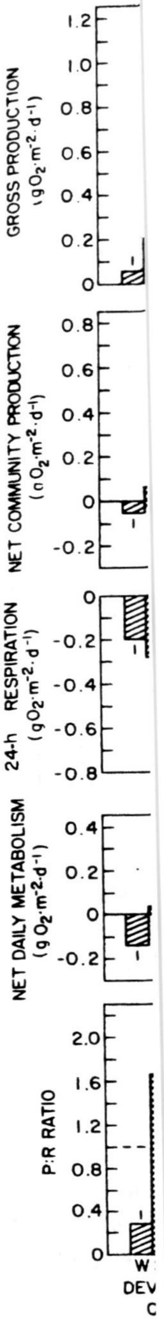


FIG. 8. Metabolism per unit of weight for detritus in Fig. 7 combined with the mean seasonal standing crop of CPOM and FPOM (Naiman and Sedell 1980) to estimate metabolic activity by the total detritus component. Symbols are described in previous figures.

TOTAL STREAM METABOLISM

The highest metabolic rates for Devils Club Creek, Mack Creek, and Lookout Creek are in spring and summer when light levels and periphyton activity are near maximal (Fig. 9). Gross production ranges from about 0.2 g $O_2 \cdot m^{-2} \cdot d^{-1}$ in Devils Club Creek to about 0.8 g $O_2 \cdot m^{-2} \cdot d^{-1}$ in Lookout Creek and the McKenzie River. Overall, metabolic rates in Devils Club Creek and Mack Creek are only about half those measured in the larger streams, except for Mack Creek in summer when metabolism is equal to levels measured



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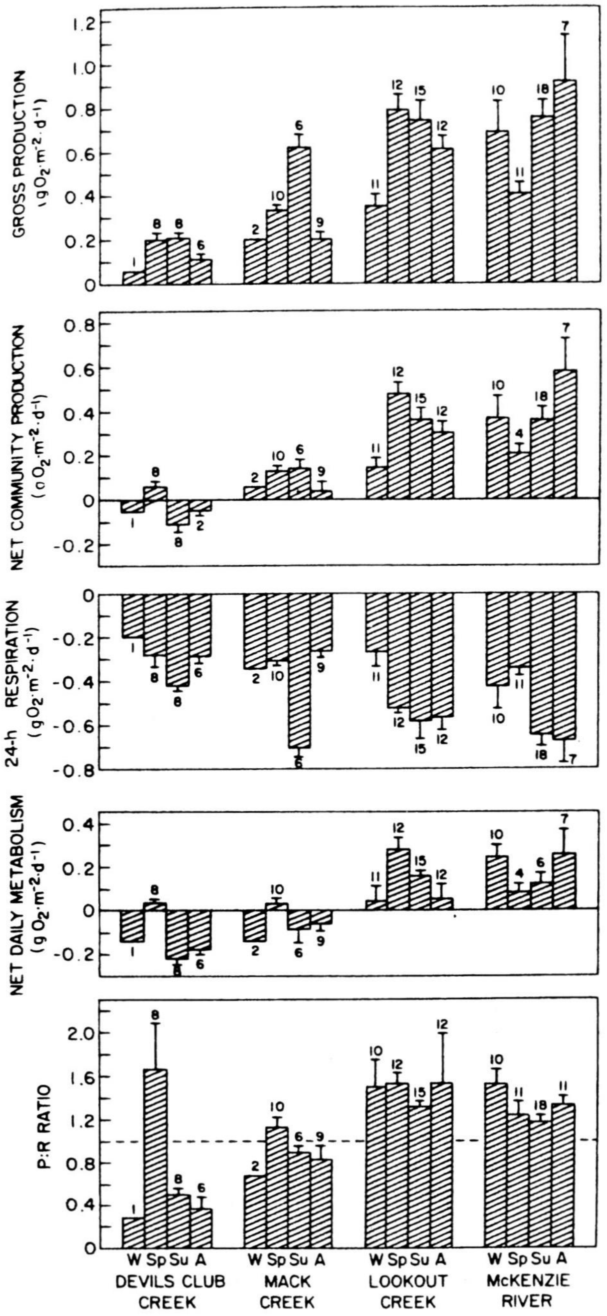

FIG. 9. Total metabolism by each stream on an areal basis estimated by combining the periphyton component with total detritus. Symbols are explained in other figures. Respiration by the animal community is not included; it is usually only a small part of the total.

in the largest streams. The McKenzie River has a relatively low metabolic rate in spring coinciding with peak discharge. Net community production and net daily metabolism are positive for all seasons in Lookout Creek and the McKenzie River (Fig. 9). Diel respiration generally increases in a downstream direction but differences between low- and high-order streams are not great; all sites respire between 0.2 and 0.7 g $O_2 \cdot m^{-2} \cdot d^{-1}$. Except during spring, when light levels are relatively high, Devils Club Creek and Mack Creek have P:R ratios <1. Lookout Creek and the McKenzie River have P:R ratios >1 with little annual variation.

SYNTHESIS

Comparisons with other streams — Streams examined in this study have some of the lowest production rates recorded to date but the values are comparable to other mountainous Oregon streams. Hansmann et al. (1971) reported gross production in Drift Creek, Oregon, ranging from 0.5 to 2.5 g $O_2 \cdot m^{-2} \cdot d^{-1}$, while Lane (1965) found gross production rates of 0.4 to 1.1 g $O_2 \cdot m^{-2} \cdot d^{-1}$ in 2nd-order Needle Branch, Oregon, and 0.4 to 1.3 g $O_2 \cdot m^{-2} \cdot d^{-1}$ in 3rd-order Flynn Creek, Oregon. Net production rates for Carnation Creek and Ritherdon Creek, British Columbia, two rain forest streams, are identical with rates in Devils Club Creek and Mack Creek (0.1 g $O_2 \cdot m^{-2} \cdot d^{-1}$) and are possibly the lowest ever measured for a stream ecosystem (Stockner and Shortreed 1976).

Although not specifically studied here, some insights can be given to factors controlling metabolism in western Oregon streams. In all streams, metabolism will be affected by light and nutrient availability, temperature, and the hydrologic regime, with the relative importance of each factor varying from stream to stream. Major controlling factors in smaller streams are most likely the hydrologic regime and light availability. When forests associated with small streams are clearcut, light availability and nutrients are increased. Nutrient leaching is completed in a few years while light remains at increased levels for many years thereafter (Hansmann and Phinney 1973; Stockner and Shortreed 1976). Primary production in these situations is enhanced remaining at relatively high levels several years after logging (Gregory 1979). Nutrients are dilute in the streams we studied (Naiman and Sedell 1979), probably limiting production in the larger streams where more light is available. McIntire and Phinney (1965) investigated effects of temperature on metabolism in streams finding dramatic changes with a ΔT of 10°C. Normally temperatures range from about 2 to 15°C during the year for all sites but total metabolism in these streams did not reflect these temperature changes, indicating the biota possibly undergo some temperature compensation with season.

Downstream trends in stream metabolism — From this study it is apparent that total benthic community metabolism per unit area increases as streams become larger, detritus metabolism per unit of weight remains the same regardless of stream size, total detrital metabolism decreases as streams become larger because there is less detritus downstream, periphyton production increases with stream size because of greater light availability downstream, and the P:R ratio is >1 in downstream reaches, and can be >1 for short periods in the smaller streams depending upon the season. Total community metabolism is largely determined by the amount of detritus and associated periphyton in small streams, and mostly by the activity of periphyton alone in larger streams.

A good understanding of the community structure and physiological functions of stream ecosystems requires that major sources of organic matter and their fate within the system be known. At this time it is almost a paradigm that stream ecosystems are heterotrophic (Fisher and Likens 1973; Cummins 1974; Hynes 1975) despite extensive evidence that many streams can have an autotrophic base (Minshall 1978). Most communities in small streams appear to depend predominantly upon organic matter imported from adjacent terrestrial systems for their energy base because, to date, most ecological studies of streams have been conducted in temperate regions where forests provide abundant allochthonous energy sources and extensive shade, thereby appearing to minimize the importance of autochthonous photosynthesis. In small streams without extensive forest canopies or with suitable substrates for periphyton, or in larger streams where the forest canopy is open, autotrophic processes are important (Minshall 1978). Thus, all streams should not be considered heterotrophic, but rather the relative importance of heterotrophic and autotrophic processes should be critically evaluated. Minshall (1978) tabulated 40 P:R ratios finding values amost equally divided between those indicating heterotrophy and those indicating autotrophy. We summarized data from 27 streams finding that over a wide geographical area streams from orders 1 to 7 cannot be classified as either autotrophic or heterotrophic based on order alone. The relative importance of heterotrophy and autotrophy will depend upon the magnitude and character of detrital inputs, forest canopy development, the physical regime, and light availability.

Other trends seen in this study, such as total metabolism and P:R increasing in a downstream direction, have not been observed by other investigators but they have been postulated by Fisher (1977) and Vannote et al. (1980). Hoskin (1959) examined six sites in the Neuse River system, North Carolina, ranging from about a 2nd-order stream to approximately a 6th-order stream at the estuary, and only in the estuary was there a sharp increase in productivity. In this study metabolism and P:R showed no discernible trend with stream size. Likewise, in a short section of New Hope Creek, North Carolina, there was no seaward increase in gross production (Hall 1972).

Unfortunately, we did not choose a wide enough range of sampling stations to test completely the original hypothesis proposed by Cummins (1975, 1977). In general, the hypothesis appears to be correct for streams within a biome, ranging up to a moderately large river. It remains to be demonstrated, however, if the P:R ratio will again decrease to <1 in larger rivers where light attention due to depth and the metabolic activity of fine seston are major factors determining ecosystem metabolism.

Acknowledgments

We thank K. Luchessa, C. Hawkins, and D. McCullough for their excellent assistance with the sampling program, Woolcott Smith and Sandra George for statistical analysis, Gloria Blair for preparing the illustrations, and the National Science Foundation for financial support (BMS 75-0733). Substantial improvements were made to the manuscript through thoughtful discussions and comments from T. D. Bott, M. R. Church, K. W. Cummins, C. E. Cushing, S. G. Fisher, S. V. Gregory, C. P. Hawkins, and G. W. Minshall. This is contribution No. 11 from the River Continuum Project.

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