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Dynamics of detritus in a small stream in southern Sweden and its influence on the distribution of the bottom animal communities

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Transport and availability of various size fractions of organic material along with bottom structure and benthic invertebrates, grouped with respect to feeding types, were examined along an 8 km long stream in southern Sweden. Transport of coarse particulate organic material (CPOM) was insignificant, while considerable amounts of fine particulate (FPOM) and dissolved organic matter (DOM) were carried downstream. DOM showed little variation and was constantly 2–3 times the energy of suspended FPOM. Export of DOM was 5 times as high as that of FPOM, total organic output being twice as high as leaf input. On a stony bottom shredders and scrapers dominated, whereas scrapers, deposit feeders and filter feeders were abundant where sedimentation was heavy. Downstream the section with most extensive sedimentation all categories including predators were well represented.

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Проводили исследование транспорта и доступности различных фракций органического материала в зависимости от структуры дна и типа питания бентосных беспозвоночных на протяжении 8 км русла реки в южной Швеции. Транспорт грубо размельченного органического материала (CPOM) незначителен, но мелкие частички (FPOM) и растворенное органическое вещество (DOM) переносятся вниз по течению. DOM мало изменчив и постоянно содержит 2–3 кратный запас энергии в сравнении с FPOM. Экспорт DOM в 5 раз выше, чем поступление листвы. На каменистом дне преобладают глотатели и скребущие формы, в то время как скребущие, потребители осадка и фильтраторы – в местах, с плотным осадком. Вниз по течению отмечен участок с наиболее экстенсивным осаждением, где встречаются все группы, включая хищников.

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1. Introduction

The dependence of stream animal communities on allochthonous detritus has been documented in a number of studies (Hynes 1975). In temperate regions the input of organic matter is largely restricted to a short period of autumnal leaf fall. As pointed out by Ross (1963), the life cycles of many stream detritivores are clearly adapted to seasonal fluctuations in the availability of decaying leaves. A variety of functionally different organisms from bacteria and fungi to large insect larvae are simultaneously engaged in the breaking down of the allochthonous detritus (Petersen and Cummins 1974, and Sedell et al. 1975). The transfer of energy along food chains and the temporal differences of energy availability along with the special conditions of an unidirectional flow of the ambient medium are central features in recently developed views of streams as continua (Vannote 1975 in Cummins 1975) or successional sequences (Margalef 1968).

Many efforts have been made to explain the gradual change or zonation of animal communities along water-courses (Illies 1961, Allan 1975, Hawkes 1975; see also Hynes 1970 for a review). However, although temporal changes in detritus abundance have been taken into account in many studies, little attention has been paid to spatial patterns of detritus dynamics. One notable exception is that of Reice (1974) who related environmental patchiness in a stream to the rate of leaf litter breakdown. And still, to explain the distribution of benthic species and of animal communities within streams, one would suspect spatial differences of detritus abundance to be of primary importance. The aim of the present study is to analyse this variable, using data of the availability and dynamics of different detritus fractions as a basis for explaining the distribution of single species or sets of species along the water-course.

2. Study area

The Stampen stream (approx. 55°37′N, 13°35′E) has been the subject of several investigations (see e.g. Hultin 1971, Otto 1971, 1974, Svensson 1975, Svensson 1977, Malmqvist 1978). This small woodland stream flows to the NE from the hillsides in the central part in the province of Skåne in southernmost Sweden (Fig. 1). The Stampen stream belongs to the Kävlinge River system. The stream passes mainly through beech and alder forests and also some agricultural land. The stream is eutrophic and only slightly polluted. Some of its most important chemical features are shown in Tab. 1. The stream is approximately 8 km long and perennial. The mean water discharge is about 0.04 $m^3\ s^{-1}$. Its width varies between 0.5 and 3 m and its depth between 0.1 and 0.7 m.

Tab. 1. Range of some environmental variables in the Stampen stream.

pH	7.22–8.35
$\varkappa_{20}$ (µS)	280–480
Ca^{2+} (mg l^{-1})	50.2–74.6
PO_4^{3-} (mg l^{-1})	0.03–0.05
NO_3^- (mg l^{-1})	0.4–0.9

The temperature regime was described by Otto (1974) and Svensson (1977). The bottom substrate consists mainly of sand although, in the upper parts, stones, pebbles and gravel dominate. Aquatic vegetation is generally sparse due to the shading effect of the forests, but is abundant in the lowermost section where the stream flows through pastures. Typical species include *Glyceria maxima* (Hartm.) Holb., *Epilobium hirsutum* L., *Berula erecta* (Huds.) Coville and *Sparganium* spp. In Fig. 7b the stream gradient is shown. The tributaries are few and insignificant. The stream is supported mainly by ground water discharge. The leaf litter input to the upper parts has been estimated to about 11.4 10^6 J m^{-2} yr^{-1} (680 g dry wt m^{-2} yr^{-1}) (Otto 1975).

An important feature is a ravine in the upper part of the stream. Shed leaves from the beech forest gradually fall or drift down its steep slopes and eventually enter the stream. In its middle and lower parts, the stream flows through a very flat landscape where shed leaves promptly fall into the water or blow into it from the surroundings.

3. Terminology

The organic material was separated into the following size categories. Coarse particulate organic matter (abbreviated CPOM) was the fraction containing particles with Ø > 15 mm. Medium sized particulate organic matter (MPOM) was subdivided into particles 6–15 mm and 1–6 mm, respectively. Fine particulate organic matter (FPOM) comprised all particles between 0.45 µm and 1 mm. Organic material less than 0.45 µm was defined as dissolved organic matter (DOM).

4. Material and methods

4.1. Field sampling

The program was run from early November 1975 until early December 1976. In each month except June all of the following sampling routines were carried out except the bottom fauna sampling, which was performed only in December 1975 and April and September 1976.

4.1.1. CPOM on the bottom

At 6 locs, viz. 1, 3, 7, 12, 16 and 17 (see Fig. 1) sections of the stream were selected. Each section encompassed the total width of the stream and a length of 5 to 8 m (areas between 7 and 11 m^2). A large net (mesh size 1

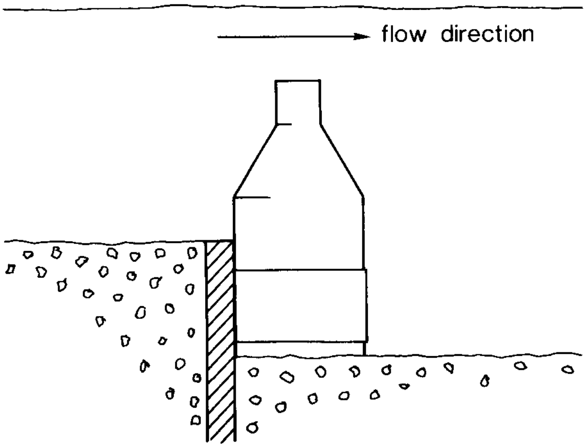

Fig. 2. Lateral view of bottle arranged for sampling suspended FPOM.

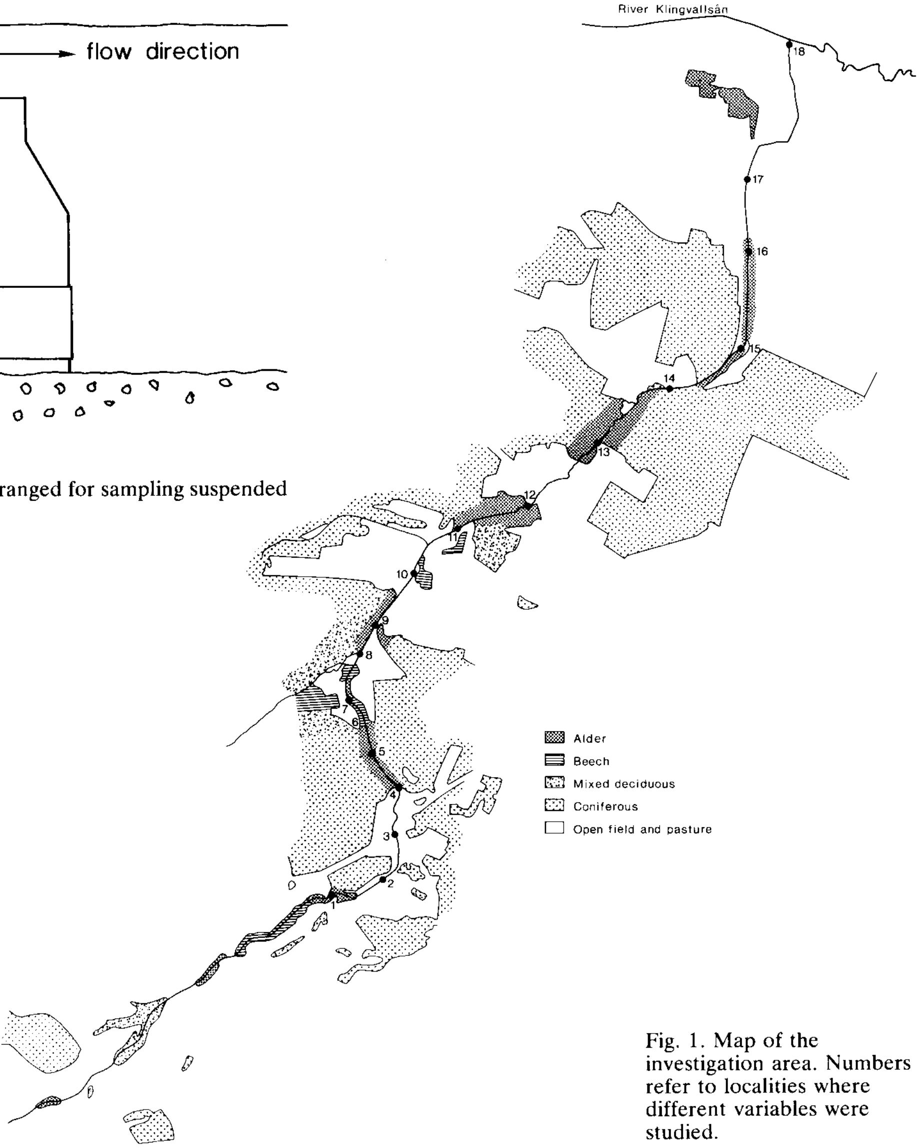

Fig. 1. Map of the investigation area. Numbers refer to localities where different variables were studied.

mm) was arranged in the downstream end of each section and all organic material within the section was collected in the net. The material was transported in large polythene bags to the laboratory for further treatment.

4.1.2. FPOM in the sediment

At 4 locs, viz. 1, 7, 12 and 16 the amount of FPOM on the bottom was estimated using a core sampler (diam. 0.12 m, height 0.03 m). The sampler covered an area of 113 cm^2 and each sample had a volume of 340 cm^3. At each locality 10–20 samples were taken and transported to the laboratory in polythene bags.

4.1.3. FPOM in suspension

At each of all 17 localities three plastic bottles were stuck into the bottom and kept in position by a piece of wood with metal holders. The bottles were placed vertically so that the apertures were exposed to the current at 5–10 cm above the bottom (Fig. 2). The bottles acted as traps for material suspended in the water. The volume of the material settling during one month was assumed to be dependent on current, depth and concentration of FPOM in the water. The influence of depth was tested in the field and found to be of minor importance provided the apertures were situated more than 5 cm above the bottom surface. Thus, only current speed and concentration of FPOM had to be taken into account when the method was calibrated in the laboratory. When bottles were exchanged, the water current was measured in a standardized way with a Grant Miniflow meter, close to the aperture of the bottle. The volumes of FPOM in the bottles and current speeds were entered on a graph based on calibrations made in the laboratory (see below) (Fig. 3).

4.1.4. DOM

Water samples were collected at 5 locs, viz. 1, 3, 7, 12 and 16. They were analysed by means of wet-oxidation (Maciolek 1962) to estimate their energy content. Fifty ml of water was previously filtered (Millipore 0.45 μm) to assess the energy content of DOM and another 50 ml of water was treated unfiltered to give the total energy content. The difference was regarded as FPOM.

4.1.5. Bottom fauna sampling

At 6 locs, viz. 1, 2, 7, 12, 16 and 17, the bottom fauna was sampled with a Neill sampler (Neill 1938), covering an area of 500 cm². Six – ten samples were taken at each locality and immediately preserved in 70% ethanol.

4.2. Laboratory treatment

4.2.1. CPOM on the bottom

The collected material was wet sieved in a channel (length 5 m, width 0.4 m, height 0.4 m). Three different sieves were used, viz. 15 mm, 6 mm and 1 mm. Organic material divided into these fractions was dried at room temperature and weighed to the nearest gram. The material > 15 mm was subsampled and the frequency of leaves from different tree species determined.

4.2.2. FPOM in the sediment

Each sediment sample was flotated and organic fractions transferred into Imhoff funnels, graded in ml. To speed up sedimentation in the funnels, hot water was used. The volume of the organic material was measured to the nearest ml. A volumetrically constant subsample was dried at 60°C. The correlation between volume and ash-free dry weight was established.

4.2.3. FPOM in suspension

The content in the bottles was sieved through a 1 mm net and flotated in hot water to reduce the amount of inorganic material. The remaining fraction was treated as in Sect. 4.2.2.

The bottle method was calibrated against different concentrations of FPOM and current speeds in a circular aquarium (diametres: outer rim 0.80 m, inner rim 0.25 m and height 0.40 m). In this a constant current was produced by a paddle. FPOM collected in the stream was added to the water and allowed to settle. Equilibrium concentrations of FPOM were then established according to the current produced by the paddle. A bottle similar to those used in the field was then immersed into the water and emptied every six hours. The volume of organic material in the bottle was estimated in Imhoff funnels. The bottle trapped FPOM from the water so that the concentration was successively lowered until approx. 5 mg l⁻¹ when the experiment was terminated.

Concentrations of FPOM suspended in the aquarium were determined by filtering 50 ml samples of water through preweighed Millipore filters (0.45 μm), drying the filters and weighing again. The relationships between concentrations of FPOM in the water, amount of FPOM in the bottle, and water current were used for the construction of a calibration curve (Fig. 3). The three samples of FPOM from each locality showed close agreement regarding concentration of FPOM in the water when corrected for current, indicating a lateral uniformity of FPOM in the water.

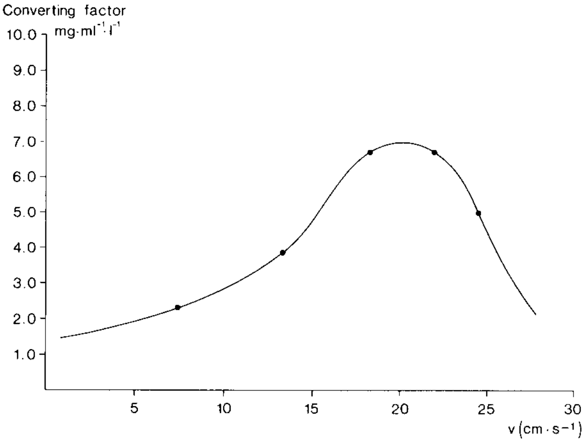

Fig. 3. Efficiency of bottles for sampling FPOM in relation to water velocity. For a given water velocity, multiply the corresponding converting factor (read off from the ordinate) with the amount of FPOM (in ml) obtained from the bottles in the field. The product provides an estimate of the averaged concentration of FPOM in the water over the period measured (corrected for days of exposure).

4.2.4. Bottom fauna sampling

All samples were handsorted and the animals determined to species level (except for Diptera, Tubificidae and Acari). Species or other taxa were grouped into 5 functionally different categories, viz. shredders, collectors-filter-feeders, collectors-sediment-feeders, scrapers and predators. The classification of the animals on functional groups corresponds to that of Cummins (1973). The animals were dried at 60°C and weighed.

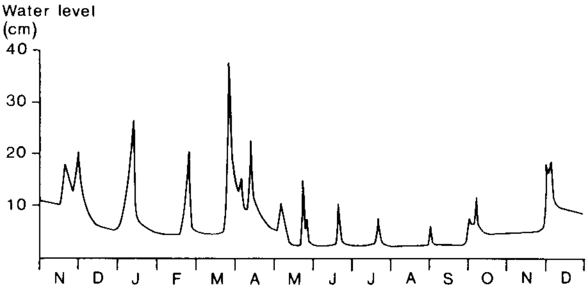

Fig. 4. Water level at locality 7.

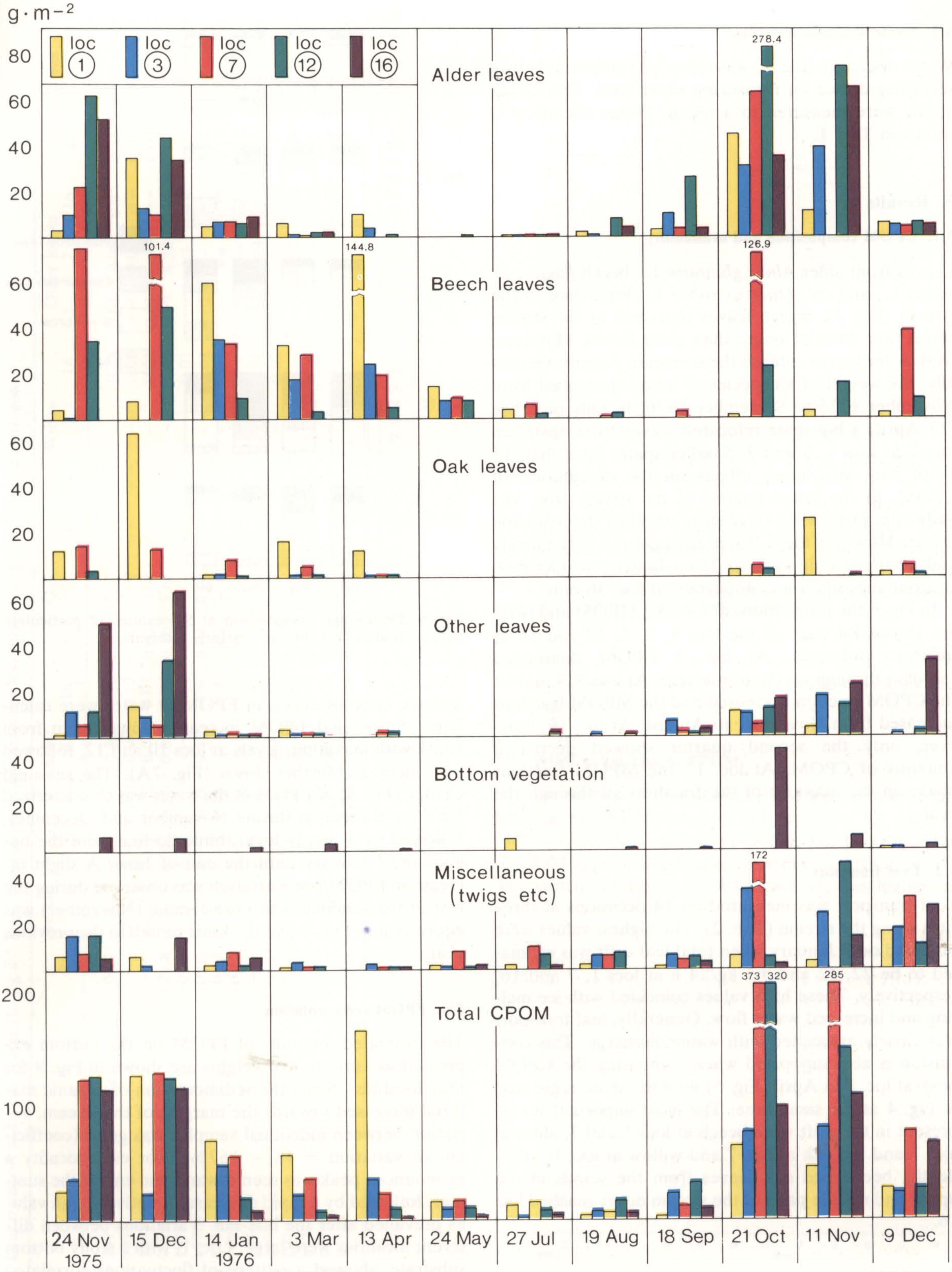

Fig. 5. Available CPOM (g dry wt m^{-2}) at localities 1, 3, 7, 12 and 16. At locality 17, situated approximately 400 m downstream of locality 16, there was no CPOM present on any sampling occasion.

4.3. Environmental variables

Water discharge (Fig. 4) was recorded continuously by a recording device for measuring water level. The fluctuations were measured in a notch. Water chemistry is shown in Tab. 1.

5. Results

5.1. CPOM composition and availability

Leaves from alder *Alnus glutinosa* L., beech *Fagus sylvatica* L., and oak *Quercus robur* L. dominated in the stream (Fig. 5). Beech leaves remained in the stream about four months longer than alder leaves. However, fresh alder leaves entered the stream in August. Generally, the weight of all species of leaves decreased from November 1975 to September 1976. In only one case (13 April) a big spate relocated leaves from upstream loc. 1 to locs 1, 3 and 7. Smaller spates later than 13 April had only minor effects on the distribution of CPOM. In the lower regions of the stream (loc. 16) *Salix* spp. provided a large proportion of the available leaves. However these leaves disappeared very quickly and occurred only sparsely from January to October. Bottom vegetation was important at loc. 16 only.

In Fig. 6 the proportions of CPOM, MPOM and twigs are shown for each of the locs 1, 3, 7, 12 and 16 at quarterly intervals. At loc. 1 CPOM dominated (>60%) throughout the whole year. At locs 3, 7 and 12 the CPOM fraction decreased and the MPOM fractions increased from November to August. At loc. 16, however, only the second quarter showed decreased amounts of CPOM. At loc. 12 the MPOM fractions made up the majority of the fractions all through the year.

5.2. Leaf transport

Leaf transport was measured on 14 occasions at three sites along the stream (Tab. 2). The highest values were obtained on 9 January when total leaf drift was estimated to be 22, 42 and 9.5 kg/24 h at locs 1, 7 and 16, respectively. These high values coincided with ice melting and increased water flow. Generally, leaf transport was closely associated with water discharge. This conclusion is also supported when comparing the CPOM peak at loc. 1 in April (Fig. 5) with the spate registered in Fig. 4 at the same time. The most important leaves present in the drift were beech at locs 1 and 7, alder at locs 7 and 16, oak at loc. 7 and willow at loc. 16. Evidently, beech and oak leaves from the stands in the upper and middle parts of the stream never reached loc. 16.

5.3. FPOM transport

Average water current, amount of FPOM in bottles and average concentrations of FPOM in water were calculated. Suspended FPOM increased downstream from loc. 1 with maximum levels at locs 10 and 12, followed by a decrease further down (Fig. 7A). The seasonal change (Fig. 8) of FPOM in the water was characterized by a rapid increase during November and December, followed by a nearly logarithmic decline from the beginning of January until the end of June. A slight increase in FPOM concentration was observed during the rest of the summer. The lowest value (November) was equivalent to that found the same month in the previous year.

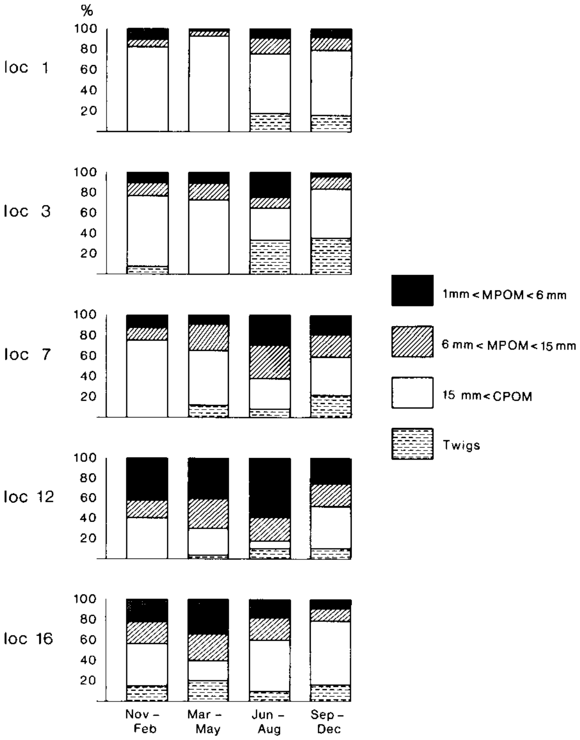

Fig. 6. Percentage composition at 5 localities of particulate organic matter > 1 mm at quarterly intervals.

5.4. FPOM sedimentation

The estimated amounts of FPOM on the bottom expressed as ash-free dry weights are shown in Fig. 9 for four localities. Since the sedimentation of organic material increased towards the margins of the stream, variation between individual samples was great (coefficient of variation = 48 – 167%). For each locality a pronounced peak was seen towards the end of the summer, followed by a rapid decrease. Relatively high values prevailed after the leaf-fall. Variations between different localities were large. Loc. 1, with a stony bottom substrate, showed a pattern of fluctuations correlated with water level conditions. At loc. 7, with a high gradient and a very unstable substrate the variations were

Tab. 2. Leaf transport at locs 1, 7 and 16. Kg d^{-1}. (++): leaves present in amounts less than 10 g. (– –) leaves not present.

Date	Beech			Alder			Oak			Willow			Other leaves			Total leaves		
	1	7	16	1	7	16	1	7	16	1	7	16	1	7	16	1	7	16
20 Nov 1975	0.01	2.64	++	0.06	0.33	0.96	0.07	0.27	– –	– –	– –	0.28	0.01	0.08	0.05	0.15	3.32	1.29
1 Dec 1975	– –	0.27	– –	0.02	0.07	0.13	– –	0.07	– –	– –	– –	0.06	– –	0.03	– –	0.02	0.44	0.19
17 Dec 1975	– –	0.14	– –	0.02	0.01	0.01	0.01	0.01	– –	– –	– –	0.01	0.01	– –	– –	0.04	0.16	0.02
9 Jan 1976	20.8	23.7	0.05	0.96	6.62	5.04	0.10	5.62	– –	– –	– –	4.42	0.19	6.38	– –	22.0	42.3	9.51
9 Feb 1976	0.01	0.01	++	– –	– –	0.01	– –	– –	++	– –	– –	0.01	– –	++	++	0.01	0.01	0.02
3 Mar 1976	0.05	4.38	– –	0.01	0.12	– –	0.04	0.24	– –	– –	++	0.01	0.01	– –	– –	0.11	4.74	0.01
24 Apr 1976	0.13	0.08	– –	0.01	– –	– –	0.04	++	– –	– –	– –	– –	++	++	0.06	0.18	0.08	0.06
25 May 1976	0.12	0.11	– –	– –	0.01	++	++	– –	– –	– –	– –	– –	– –	– –	– –	0.12	0.12	++
27 Jul 1976	– –	– –	– –	– –	– –	0.02	– –	– –	– –	– –	– –	0.01	0.02	0.09	0.02	0.02	0.09	0.05
19 Aug 1976	– –	– –	– –	– –	– –	0.07	– –	– –	– –	– –	– –	0.02	– –	– –	0.01	– –	– –	0.10
18 Sep 1976	– –	0.02	– –	0.04	0.02	0.32	0.01	++	++	– –	– –	0.04	– –	0.02	0.07	0.05	0.06	0.43
21 Oct 1976	– –	0.23	– –	0.26	0.10	0.08	0.01	0.07	– –	– –	– –	0.03	0.04	0.05	0.02	0.31	0.45	0.13
11 Nov 1976	– –	0.25	– –	0.02	0.06	0.06	0.02	0.01	– –	– –	– –	0.13	– –	0.06	0.01	0.04	0.38	0.20
9 Dec 1976	0.01	0.69	++	0.02	0.08	0.02	0.01	0.05	++	– –	– –	0.03	0.01	++	– –	0.05	0.82	0.05

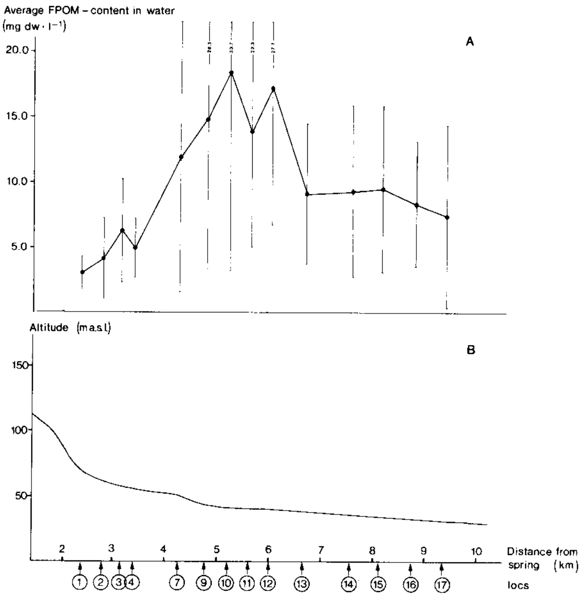

Fig. 7A. Concentration of FPOM in suspension at 14 localities along the stream. The values are given in mg dry wt l^{-1}. Mean ash content of the material was 54 ± 7%. Each dot represents a mean of 14 measurements obtained from Nov 1975 to Dec 1976. Vertical bars denote S.D. 7B. The gradient of the Stampen stream plotted from a topographic map.

irregular. Locs 12 and 16 with low gradients generally had high values.

5.5. DOM in relation to FPOM

The proportion of DOM and FPOM was considered by pooling water samples from all occasions for each of locs 1, 3, 7, 10, 12 and 16 (Fig. 10). The concentration of DOM appeared to be very constant at 230–270 J l^{-1}. The concentration of FPOM, however, was highest at

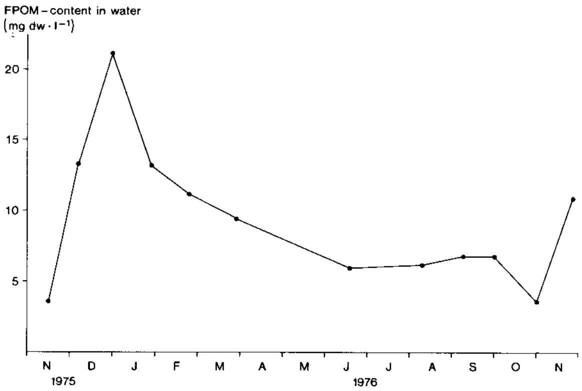

Fig. 8. Concentration of FPOM in suspension for the period November 1975–November 1976. Each dot represents a mean of all localities sampled on each occasion.

Tab. 3. Benthic animal abundance (no. m^{-2}) and subdivision into functional categories in the Stampen stream. Data are given from six localities on three sampling occasions.

	1 Dec 1975						22 Apr 1976						18 Sep 1976					
	1	3	7	12	16	17	1	3	7	12	16	17	1	3	7	12	16	17
Shredders																		
Plecoptera																		
Capnia bifrons (Newm.)	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nemoura avicularis (Mort.)	-	-	-	-	180	5	-	-	-	-	-	-	-	-	-	-	387	-
N. cinerea (Retz.)	-	-	-	-	-	-	-	4	8	4	-	8	-	-	-	-	-	-
N. flexuosa (Aub.)	-	-	4	12	4	20	12	4	8	-	-	4	-	-	27	-	7	-
Taeniopteryx nebulosa (L.)	-	-	-	16	124	20	-	-	-	-	-	-	-	-	3	-	633	43
Trichoptera																		
Chaetopteryx villosa (Fbr.)	4	10	-	-	48	20	12	4	-	-	-	28	-	-	-	3	3	-
Halesus digitatus (Schrk.)	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-
H. radiatus (Curt.)	-	-	-	4	4	-	-	-	8	-	-	-	-	3	-	-	-	-
H. tesselatus (Ramb.)	-	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-
Limnephilus lunatus (Curt.)	-	-	-	-	-	30	-	-	-	-	-	-	-	-	-	-	-	-
Potamophylax cingulatus (Steph.)	40	44	16	68	56	-	-	-	4	4	-	4	-	-	-	-	13	-
P. nigricornis (Pict.)	-	-	-	-	-	-	4	-	-	-	-	-	17	3	-	-	-	-
Sericostoma personatum (Spence)	4	6	-	-	-	-	-	8	-	-	-	-	70	13	-	-	-	-
Total number of shredders	56	60	20	100	416	100	28	20	28	8	0	44	90	19	30	3	1043	43
Scrapers																		
Crustacea																		
Gammarus pulex (L.)	2364	3076	260	1788	836	335	1640	2644	328	648	268	716	1603	6960	1187	127	1107	523
Ephemeroptera																		
Baetis niger (L.)	-	-	-	-	16	-	-	-	-	-	28	4	-	-	-	-	-	-
B. rhodani (Pict.)	288	146	12	160	164	145	264	496	108	12	8	96	13	3	-	27	-	17
Plecoptera																		
Brachyptera risi (Mort.)	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-
Coleoptera																		
Elmis aenea (P. Müll.)	-	-	-	-	16	10	-	-	-	-	-	12	-	-	-	-	20	3
Haliplus lineaticollis (Mrsh.)	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	847
Helodes minuta (L.)	104	6	-	-	-	-	-	-	-	-	-	-	177	3	133	-	-	-
Limnebius truncatellus (Thunb.)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	20	-	-	-
Limnius volckmari (Panz.)	4	50	-	-	4	-	4	32	-	-	4	-	47	3	-	-	20	7
Trichoptera																		
Silo pallipes (Fbr.)	12	-	-	-	-	-	20	4	-	-	-	-	3	-	-	-	-	-
Mollusca																		
Ancylus fluviatilis (Müll.)	-	-	-	-	4	4	4	-	-	-	-	-	3	-	-	-	-	-
Lymnaea peregra (Müll.)	-	-	-	-	-	68	-	-	-	-	-	12	-	-	-	30	-	77
L. truncatula (Müll.)	-	-	-	-	-	4	-	-	-	-	4	8	-	-	-	-	-	-
Total number of scrapers	2772	3278	272	1948	1040	562	1936	3176	436	660	312	854	1846	6969	1340	184	1147	1474
Deposit feeders																		
Oligochaeta																		
Eiseniella tetraedra (Sav.)	8	2	-	24	4	4	-	8	-	8	-	-	7	-	-	20	7	-
Tubificidae	4	6	0	140	-	220	8	4	-	112	-	236	37	-	70	503	-	407
Crustacea																		
Ostracoda	-	-	-	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Ephemeroptera																		
Brachycercus harrisella (Curt.)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-
Ephemera danica (Müll.)	4	38	16	-	700	5	-	28	32	-	84	24	-	97	20	-	1373	27
Coleoptera																		
Hydraena gracilis (Germ.)	-	-	-	-	-	-	4	-	-	-	-	-	3	-	-	-	-	-
Diptera																		
Ceratopogonidae	-	2	-	-	8	10	-	-	-	-	-	24	20	10	-	3	63	140
Chironomidae	1720	40070	328	7568	18456	560	968	148	188	2644	1092	15864	1360	2038	620	4833	1173	3120
Ptychopteridae	8	276	76	236	60	5	-	192	16	96	-	-	10	227	60	13	-	-
Tabanidae	-	4	8	12	-	100	-	-	-	12	-	20	-	-	117	23	37	87
Tipulidae	92	274	100	112	128	295	32	136	68	76	112	76	260	100	97	17	263	27
Other Diptera	-	6	-	4	12	-	-	-	-	4	8	12	-	-	-	3	17	63
Cyclostomata																		
Lampetra planeri (Bloch)	-	-	-	-	4	-	-	-	-	-	-	-	-	3	-	-	23	-
Total number of deposit feeders	1836	40678	528	8104	19372	1199	1012	512	304	2952	1296	16256	1697	2475	964	5415	2959	3871
Filter feeders																		
Trichoptera																		
Hydropsyche pellucidula (Curt.)	-	-	-	-	4	15	-	-	-	-	-	28	-	-	-	-	-	-
Lype reducta (Hag.)	-	-	-	-	20	-	-	-	-	-	-	-	-	-	-	-	-	-
Diptera																		
Simuliidae	80	42	-	36	32	70	40	16	40	4	-	12	-	-	-	-	-	-
Dixidae	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mollusca																		
Pisidium sp.	-	44	12	684	612	896	-	36	-	36	60	208	100	127	-	223	57	163
Total number of filter feeders	84	86	12	720	668	981	40	52	40	40	60	248	100	127	-	223	57	163
Predators																		
Hirudinea																		
Glossiphonia complanata (L.)	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	53	-	-
G. heteroclita (L.)	-	-	4	8	-	-	-	-	-	-	-	-	3	-	-	50	-	27
Helobdella stagnalis (L.)	-	-	-	16	-	-	-	-	-	-	-	-	-	-	-	77	-	10
Neuroptera																		
Sialis lutaria (L.)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3
Trichoptera																		
Plectrocnemia conspersa (Curt.)	-	4	-	-	-	-	4	-	-	8	-	-	-	-	-	-	-	-
Polycentropidae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3
Rhyacophila fasciata (Hag.)	-	-	-	-	-	-	16	-	-	-	-	-	-	-	-	-	13	3
Coleoptera																		
Platambus maculatus (L.)	-	10	-	8	64	-	-	-	-	-	-	-	-	-	-	297	390	20
Ilybius fuliginosus (F.)	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	3
Arachnidae																		
Acarina	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	33	507
Total number of predators	-	14	4	40	64	-	20	-	-	8	-	-	3	-	-	477	436	576

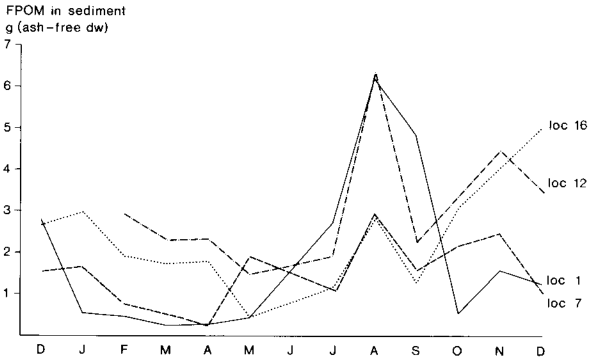

Fig. 9. Amounts of FPOM in the sediment at localities 1, 7, 12 and 16. Each value represents a mean of 10–20 samples. Coefficient of variation is given in text.

Tab. 4. Energy input and output as J yr^{-1} in the Stampen stream.

	Input	Output
CPOM	$18.1 \cdot 10^{10}$	0
FPOM[1]	Not measured	$7.3 \cdot 10^{10}$
DOM[2]	Not measured	$36.6 \cdot 10^{10}$

1. Calculated from measurements of material trapped in bottles.
2. Based on monthly samples.

loc. 12. The lowest values were recorded at locs 1 and 16. Energy content of the FPOM fraction was 40–80% lower than that of the DOM fraction per volume of water.

5.6. Faunal composition

Tab. 3 shows the total number of animals in each functional category at 6 locs and on three sampling occasions. On average, shredders, filter feeders, deposit feeders and predators were comparatively abundant at downstream localities, whereas scrapers dominated in the upper reaches of the stream. The same pattern persists in Fig. 11, where total dry weight of the different animal categories is shown.

6. Discussion

The unidirectional force of the water is an important feature that distinguishes running waters from other aquatic ecosystems. The current spaces out processes that in lentic water would occur in one spot. Hence, especially degradation processes, involving either pollutants or naturally occurring organic material, are conveniently studied in lotic environments. Although approximately the same amounts of leaf material per unit area enter different parts of the Stampen stream during leaf fall, deviations from the uniform distribution of various fractions were found and indicated which processes were involved in the transport of allochthonous material.

Two factors seem to be of primary importance for the transport of leaf material. First of all, the size of the particles influences their probability of being trapped on the bottom or carried by the water, respectively. Thus, with respect to the CPOM fraction, the distribution of certain species of leaves in the drift and bottom samples demonstrated that these leaves were transported only short distances before becoming trapped again or embedded in the substrate. This is consistent with the findings of Hall (1972) who reported that much more energy as leaves was used in situ than transported downstream. On the other hand, small size fractions, as shown in Fig. 7A. drifted for longer distances and settled further downstream.

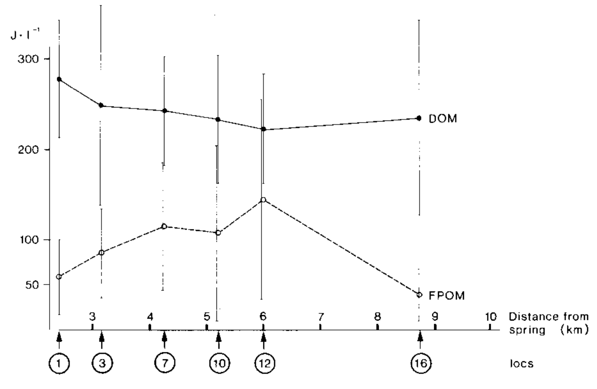

Fig. 10. Comparison of energy content of DOM and FPOM in the water at 6 localities along the stream. The values were obtained by filtering water samples. Each dot represents a mean of 10 values. Vertical bars indicate S.D.

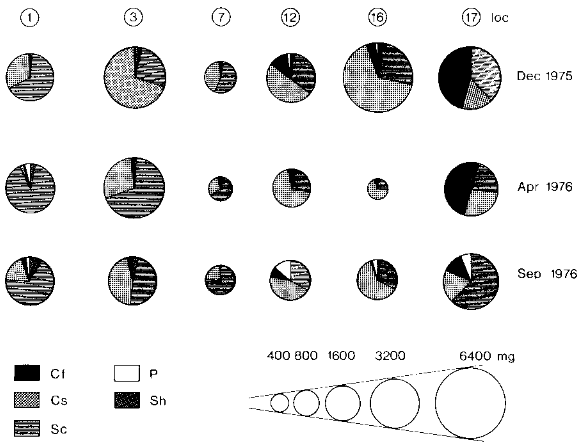

Fig. 11. Biomass (mg dry wt) and proportions of functional categories in the communities at six localities on three sampling occasions. CF = filter feeders, CS = deposit feeders, Sc = scrapers, P = predators, and Sh = shredders.

Secondly, the surrounding topography seems to influence the input of detritus. Sedell et al. (1973) found that the quantity of organic material blown into the river was 1.5 times that of the litter fall entering directly into two streams in Oregon, while Fisher and Likens (1972) only found about one quarter of the total leaf input to be due to wind transport. McDowell and Fisher (1976) considered the high values from the Oregon streams to be due to the steep stream banks. This conclusion is supported by our observations. It may also be pointed out that beech leaves are much more easily wind-transported than e.g. alder leaves.

In streams running through deep valleys the input of leaves from the surroundings occurs long after abscission. A stony streambed will trap the leaves and large leaf packs will form. A large amount of the fine material will, however, be washed out. This means that the stream gradient more directly affects the FPOM sedimentation and can be used to predict where the fine material will be deposited (cf. Fig. 7A and 7B). In Stampen locs 10–13 are situated where the stream shifts from a high to a low gradient. The thick layers of detritus formed here were only occasionally torn up and swept away. We will subsequently refer to this area as the sedimentation area.

As pointed out, few studies have been devoted to the distribution of allochthonous material in entire streams. The only work known to us is that of Minshall (1967). However, his study stream, with approximately the same discharge as Stampen, was only 1 km long and consisted mainly of riffles. This means that his data are relevant for the upper parts of our study area only. Minshall also observed increased amounts of FPOM downstream but very few leaves drifting.

Variations in the seasonal availability of the different leaf fractions were observed along the stream. Pertinent factors in this context are time of abscission, ice and snow cover, species of leaves and water discharge. The duration of ice and snow cover varies considerably between years. During our study the stream was covered with ice from about January to March. Some snow remained until April. At the melting large amounts of leaves became exposed to wind and runoff and were transported into the stream.

The decomposition rate greatly varies between different kinds of leaves (Petersen and Cummins 1974). Thus, CPOM, mainly consisting of beech and oak leaves, made up a considerable part of the total organic material present in the upper parts, at the same time as this size fraction was nearly absent at downstream localities.

As seen in Fig. 8, the largest concentration of FPOM in the water occurred in January. High water in combination with physical abrasion of the leaves probably contributed to this increase. As indicated in Fig. 7A much of the suspended material was carried downstream and deposited within the sedimentation area. Unfortunately this deposition cannot be traced in Fig. 9, where loc. 12, although situated within the sedimentation area, shows the same pattern of fluctuations in sediment FPOM as do the upstream and downstream localities. The mixing of mineral particles and FPOM that is characteristic for a sedimentation area, in addition to the thickness of the sediments, may have partly invalidated our sampling technique at this particular locality.

During the winter, high water coupled with frequent floods brought large quantities of trapped FPOM in the upper regions into suspension. The sedimentation area received much of this material and the upstream regions were literally washed clean (cf. McDowell and Fisher 1976). When the water discharge decreased and stabilized at a more constant level at the beginning of the summer, more FPOM was successively accumulated and new banks of detritus arose (cf. de March 1976). From the middle of the summer through September a slight increase in the FPOM concentration occurred. This increase coincided with stable low water conditions prevailing during these months. A similar increase has been reported by other authors (Minshall 1967). The constant flow coupled with high temperatures (low viscosity) may favour sedimentation. On the other hand, flocculation of dissolved material may contribute to the increase of suspended FPOM (Lush and Hynes 1973). Sedell et al. (1974) reported a significant input of terrestrial insect frass falling from the canopy during these months. The concentration effect of the decreasing water volume, connected with high turnover rate and activity of the biological system, might also put more FPOM in suspension.

Boling et al. (1975) presented models to predict the appearance of different leaf fractions at different seasons. Their comparisons with field data revealed high values of FPOM in November and May. Unfortunately no data were collected between June and October. Minshall (1967) found peak values in suspended organic matter (size 4–158 μm) in January and July which closely corresponds to our findings in Stampen in January and at the end of summer.

Paerl (1974) and Lock and Hynes (1976) have pointed out DOM as an important nutritive resource for the microflora. Indeed it is the largest potential energy resource in many streams (Fisher and Likens 1972). However, the nutritive value of DOM for macrobenthos is still disputable. A few investigations, mainly on marine animals, have shown that DOM can be assimilated by animals (see review in Jørgensen 1976). It might also be added that much of the DOM entering a stream via subsurface water probably already is utilized by micro-organisms in the terrestrial surroundings so that this DOM may be largely refractory (McDowell and Fisher 1976).

The energy as DOM in Stampen (measured as J l^{-1}) were always 2–3 times higher than that of FPOM. This agrees with the contention by Fisher and Likens (1972) that a stream receives a considerable amount of energy as dissolved carbon from the surrounding terrestrial systems. This input is mainly via subsurface flow (Hewlett and Nutter 1970). McDowell and Fisher (1976) estimated the DOM input to be only 19% of the total energy input during autumn. Fisher and Likens (1972) estimated the output of Bear Brook to be 66% of the total energy input. Thirty-four percent was considered as respiratory heat loss by consumer organisms, mainly micro-organisms. In Stampen, the amount of energy leaving the system during one year may be approximately estimated (Tab. 4) using mean values of DOM concentration and discharge from the lowermost locality. The amount thus calculated ($36.6 \cdot 10^{10}$ J) is twice the energy of the leaves falling into the entire stream assuming that leaves generally contain $16.7 \cdot 10^3$ J g^{-1}.

In Stampen, there is an extended sedimentation zone, which prevents particles to leave the system except during floods. Organic material may accumulate in the sedimentation area for long periods. This means that an energy balance may not appear during 1-yr studies and that sporadic spates are a prerequisite for a balance to be achieved. DOM input through subsurface water or througfall was not measured, although a considerable amount of energy probably did enter the system via these pathways.

Several factors influence the distribution of stream benthos. Apart from chemical factors which probably explain much of the variation in composition of the benthic community between different streams (Sutcliffe and Carrick 1973, Macan 1974), bottom structure (Cummins and Lauff 1969) and water velocity (Ambühl 1959) have great influence on the variation in the animal community within a given stream. In addition Egglishaw (1964, 1969) found a positive relationship between the amount of detritus and the number of animals present on the bottom. Since the bottom of many streams is a mosaic, much of the variation in species composition along streams due to detritus dynamic processes is probably difficult to elucidate. Furthermore, spates, ice cover, and various other factors may temporarily influence the benthic community drastically. Thus, although the distribution and relative abundance of the different ecological categories remained relatively constant during the study period, heavy fluctuations were observed at single localities.

Before examining the distribution of faunal assemblages along the stream, we divided the stream into four relatively distinct areas, each differing from the other with respect to abundance of detritus or to dominating size fraction of POM. In this context, these areas may also be regarded as habitats, since organic material is not solely an energy resource for the animals, but also to a large extent determines the physical features that are intimately coupled with species distribution. The uppermost of these areas (loc. 1) is the *CPOM area*. Here a stony bottom dominates and the gradient is steep. CPOM is present all through the year. Below is the *transport area* (locs 3 and 7), characterized by a relatively rapid transport of material (organic as well as inorganic) due to the sandy substrate and steep gradient. Banks of detritus were established only during extended periods of low water conditions. The *sedimentation area* occurs where the gradient begins to level out (loc. 12). This area has been described above. Downstream of this section is the *post-sedimentation area,* dominated by sand bottom (locs 16 and 17). The amount of FPOM is low compared to that of the sedimentation area. The presence of submerged vegetation during summer and autumn is a prominent feature of this stream section.

Certain animal species are very difficult to refer to any of the ecological categories we have used. The relationship of such a species to the occurrence of different types of detritus will be hard to assess but as a shortcut to the understanding of the function of the lotic ecosystems, it may be justified.

In this study the amphipod *Gammarus pulex* was ranked as a scraper although it may more accurately be defined as an omnivore with preference for fungi growing on leaf material. As *G. pulex* represents a considerable amount of the biomass at all localities this might bias the following discussion to some extent.

In the CPOM area scrapers were clearly dominant (chiefly *G. pulex* and *Baetis rhodani*). However, also shredders (caddis and stonefly larvae) were present. The biomass and abundance changed very little between sampling occasions indicating fairly stable and diverse conditions.

In the transport area sediment feeders played a more important role. However, drastical changes were observed, e.g. at loc. 3, where banks of high organic content were present on the first sampling occasion and were later washed away by floods during winter. This gave extremely high abundances of Chironomidae in December but a normal picture of *G. pulex, B. rhodani* and Chironomidae in April and September. Quick changes in community composition signified the whole area, and biomass fluctuations occurred as well. At loc. 7, the most typical transport site, the biomass was very low. Scrapers (*G. pulex*) were always dominant but also sediment feeders occurred. Long periods of stable conditions were required to allow extensive colonization (by drifting animals from upstream) of this area.

The huge amounts of FPOM in the sedimentation area, resulting in a homogeneous substrate and probably low oxygen levels, harboured unexpectedly high numbers of animals. However, in relation to the amount of potential food, numbers and biomass were very low. It is therefore probable that a large part of the FPOM in the sediments of this reach was processed by micro-organisms. Diptera (predominantly Chironomidae and Tipulidae) and Oligochaeta, which are known to withstand low oxygen levels, were dominant on this locality.

In the post-sedimentation area the density of species and individuals was high. This is particularly interesting because much of the FPOM had been deposited further upstream. However, the fraction reaching the lower parts might be of high quality at the same time as oxygen conditions of the substrate is more favourable than in the area above. Burrowing larvae of *Ephemera danica* and *Lampetra planeri* occurred in this area and contributed to a greater vertical distribution of animals within the substratum than in the sedimentation area where most species lived at or near the bottom surface. The presence of a variety of aquatic plants may also create a more diverse habitat within the post-sedimentation area allowing, for example, sessile filter feeders such as *Hydropsyche pellucidula* to exist here.

According to our interpretations, the two most important variable influencing the animal community of the Stampen stream were environmental heterogeneity and substrate stability. Detritus as a food resource may have influenced the species composition. Another impact, however, probably was its structural modification of the bottom. Thus, Egglishaw's observations, as cited above, were not confirmed in the present study, in which "detritus" has been extended to include the fine particulate organic material. Stability characterized the CPOM, sedimentation and post-sedimentation areas, respectively, whereas environmental heterogeneity virtually was high in the CPOM and post-sedimentation areas only. From the nutritive point of view, environmental heterogeneity means that FPOM accumulates on the increased substrate area, available to the animals. Part of this material belongs to the so-called epilithic detritus. This type of detritus, although not investigated in this study, is used by animals living on solid substrates, probably because bacteria are energetically linked to the organic particles (Madsen 1972, Calow 1975).

One question frequently raised in studies concerning dynamic processes in streams is how much of the observed feature that are applicable to other streams, or to what extent the observations are valid only in the study area. In the present work this question is most important when considering the low amount of suspended material leaving the system. Although the significance of primary production increases in higher order streams (4–6) imported organic material is still of importance (Cummins 1975). Since much of the particulate organic material remains in the upper parts of a river system under normal flow conditions, the energy exported downstream must consist chiefly of DOM. However, at spates, occurring at irregular intervals, vast quantities of FPOM stored in banks may be dislodged and transported considerable distances downstream. Further investigations on the transport of organic material along streams together with more extensive studies on the importance of DOM are, however, needed before any definite conclusions can be drawn.

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