Macroinvertebrates of a beaver-altered boreal stream of Alberta, Canada, with special reference to the fauna on the dams

HUGH F. CLIFFORD, GILLIAN M. WILEY, AND RICHARD J. CASEY[1]
Department of Zoology, University of Alberta, Edmonton, AL T6G 2E9, Canada

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There were different macroinvertebrate assemblages on the face of and in beaver dams compared with beaver ponds and main stream sites. The beaver dam featured a large proportion of simuliid larvae compared with the main stream sites of this stream and with areas of other studies of beaver-altered streams. The fauna of the dams was typical of fast-flowing habitats, whereas animals of the main stream sites (including the beaver ponds) were more characteristic of slow-flowing or lentic habitats. Cluster analysis separated the dam and main stream sites for each sampling date and year of our study based on the composition of the macroinvertebrates. Although the invertebrate assemblages of the dams differed from those of the main stream sites, both habitats included similar functional feeding groups, except for a shredder found only at the dams. There are similarities between the beaver dam fauna and the faunas of debris dams, woody snags, and lake outlets. Beaver dams are important in supporting large populations of simuliids and generally in maintaining a lotic fauna in slow-moving, low-gradient boreal streams.

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Les associations de macroinvertébrés rencontrées dans les barrages de castor et à leur surface se sont avérées différentes de celles rencontrées dans les étangs créés par les barrages et dans le ruisseau. Le barrage lui-même comportait une plus grande proportion de larves de simulies que les stations d'échantillonnage du ruisseau ou que les sites d'autres études sur les ruisseaux modifiés par les castors. La faune des barrages était typique des habitats d'eau courante très rapide, alors que la faune rencontrée dans le ruisseau même (y compris les étangs créés par les barrages) était plutôt caractéristique des habitats à courant lent ou des habitats lénitiques. Une analyse de groupements basée sur la composition de la faune de macroinvertébrés a séparé les stations sur le barrage et les stations dans le ruisseau lui-même pour chaque date d'échantillonnage et chaque année de l'étude. Les associations d'invertébrés des barrages différaient de celles trouvées dans le ruisseau, mais les deux habitats comptaient des groupes trophiques semblables, à l'exceptioon d'un déchiqueteur rencontré seulement sur les barrages. Il existe des similarités entre la faune des barrages de castor et les faunes qui vivent sur les barrières de débris, dans les enchevêtrements de bois ou aux sorties des lacs. Les barrages de castor assurent le maintien de grandes populations de simulies et permettent la survie d'une faune lotique dans des ruisseaux boréaux lents à pente faible.

[Traduit par la rédaction]

Introduction

Beaver (*Castor canadensis* Kuhl) populations in North America have increased during the 20th century, and many low-gradient streams of the boreal forest now appear to be continuous successions of beaver ponds. As many as 16 dams/km have been reported from Quebec, Canada (Naiman et al. 1988). Beaver dams and the resulting impoundments can affect the structure and dynamics of stream ecosystems in several ways including (*i*) modifying habitat that influences community composition and diversity, (*ii*) altering stream morphology, (*iii*) increasing the retention of sediment and organic matter, (*iv*) creating and maintaining wetlands, (*v*) modifying nutrient cycling and decomposition dynamics, and (*vi*) modifying the riparian zone (Naiman and Melillo 1984; Francis et al. 1985; Naiman et al. 1984, 1986, 1988). These effects are especially evident in 1st- through 4th-order streams (Naiman et al. 1986, 1988). Beaver dams also create patches in streams, and Pringle et al. (1988) discuss the patch dynamics of beaver-altered areas.

In beaver ponds, typical running-water taxa may be replaced by lentic taxa (Sprules 1940; Hodkinson 1975; McDowell and Naiman 1986; and Naiman et al. 1988). Sprules (1940) found fewer insects (both numbers and taxa) emerging from a beaver pond compared with the same area when it was a preimpounded riffle. McDowell and Naiman (1986) found greater density and biomass of invertebrates in beaver ponds compared with riffles in spring and summer, but found no difference in autumn. In contrast, the density of macroinvertebrates in streams unaffected by beavers tends to be greater in riffles than in pools (Minshall and Minshall 1977).

Facets usually neglected in studies of beaver-altered systems are events on the surface of and inside the dam itself. The dam frequently consists of fresh and partly decomposed leaves, and beaver-cut sticks and small logs partially submerged in water and meshed tightly together at the base of the dam with mud and other debris. Wood and organic debris of streams provide invertebrates with a site for protection (Nilson and Larimore 1973), a source of food (e.g., Pereira et al. 1982; Culp and Davies 1985), substratum type (Dudley and Anderson 1982; Anderson et al. 1984), and a more heterogeneous habitat (Anderson and Sedell 1979).

The Bigoray River, a brown-water stream of central Alberta, presently is almost a continuous series of beaver dams for long stretches; the dams account for the stream appearing more lentic than lotic. In late summer, water can be so slow moving and the substratum of such fine particles that one might question how a lotic fauna could be maintained in the stream. Yet drift samples indicate that a lotic fauna does exist in the stream. A potential habitat for riffle organisms is where water flows over and through the wood-sediment substratum of the

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[1] Present address: Alberta Environmental Centre, Bag 4000, Vegreville, AB T9C 1T4, Canada.

dam creating a small but pronounced torrential environment. This is a habitat hitherto overlooked, and there have been few, if any, studies of aquatic invertebrates associated with the substrata of these barriers.

Beaver dams and main stream stations (including beaver ponds) of the Bigoray River were qualitatively sampled from 1985 through 1989. The purpose was to determine how the faunal composition of the dams differs (*i*) amongst dams, (*ii*) from the fauna of the main stream, and (*iii*) how the most abundant taxa of the dams change seasonally.

Study area

The North Fork of the Bigoray River, a brown-water stream of west-central Alberta, Canada, is part of the Arctic Ocean Drainage. At the study site (53°31′N, 115°26′W) it is a third-order stream. This slow-moving, meandering stream drains extensive muskeg terrain, which imparts a dark color to the water, especially in late summer. At the sampling sites, base flow in summer is about 0.80 m^3/s and in winter about 0.14 m^3/s. Maximum water temperatures rarely exceed 18°C. The terrestrial flora is typical of the boreal forest and includes black spruce (*Picea mariana* (Mill.)), willows (*Salix* spp.), poplars (*Populus* spp.) and tamarack (*Larix laricina* (Du Roi)). The stream supports populations of white sucker (*Catostomus commersoni* Lacépède), northern pike (*Esox lucius* L.), and a few burbot (*Lota lota* L.) and arctic grayling (*Thymallus arcticus* (Pallas)). A detailed description of the stream in the 1960s and 1970s is given by Clifford (1978). During the late 1970s and 1980s beaver populations increased in the drainage, and during the study (1985–1989) there were dams about every 100–200 m in the vicinity of the study area.

Two beaver dams, about 100 m apart, were chosen for the study. These sampling sites are designated dam 1 and dam 2. Each dam formed a barrier about 9 m wide across the stream. The dams were being maintained and during the study were not seasonally destroyed by high water. The stream channel is bordered on both sides by steep banks; and impounded regions, even during high water, do not normally flood terrestrial areas. Both dams were of woody material (mainly poplar), with accumulations of leaves and finer organic material, especially at the crest of the dam. Depending on the water level, water flowed over the crests of the dams or through the dams. Main stream sites 1 and 4 (M1 and M4) were located in shallow regions of the impoundments of dam 1 and dam 2, respectively, each about 2 m upstream of the dam. Samples were taken from the M4 site on only two dates. The other main stream sites (M2 and M3) were about 5–10 m downstream of dam 1 and dam 2, respectively, and represent typical main-stream stretches of this impounded stream. These sites have slow-moving water. Substratum of the main stream sites was mostly clay, silt, and sand covering a gravel–cobble substratum. There were no riffles between the dams.

Methods

Sampling

Beaver dams and main stream sites were sampled on 20 dates throughout most of the ice-free season (mid-April to mid-November) from 1985 to 1987. The dates for 1985 were as follows: 20 June, 8 and 22 July, 16 August, and 3 October; for 1986: 6 and 21 May, 3 and 18 June, 3 July, 7 and 20 August, and 6 November; for 1987: 5 and 22 May, 4 and 25 June, 15 July, 5 and 18 August. For each date, two sites for each of two dams (dam 1 and dam 2) and two sites (2–3 m from each bank) for each of the three main stream sites (M1, M2, and M3) were sampled. But because of high water levels, on two dates we only had access to one of the M3 and one of the M2 sites; and for two other dates, we had to take samples from M4 instead of M3. Additionally, in 1987, 10 dams (two dam sites each, but no main-stream sites) on the North and South Forks of the Bigoray River were sampled on 11 June to determine the faunal composition of several dams for a single date. In 1988, samples were used to determine the kinds of chironomids and other taxa found at the dam and main stream sites. In 1989, dams 1 and 2 were sampled with a finer mesh net (see below) to determine seasonal changes in the fauna during the entire ice-free season. No main stream samples were taken in 1989. The 1989 sampling dates were: 22 February; 5 and 25 April; 8, 17 and 26 May; 1, 8, 15 and 22 June; 18 and 25 July; 1 and 25 August; 1, 13 and 29 September; 13 October; and 3 November.

Samples were taken with a pond (dip) net with a mesh size of 500 μm for 1985–1988 and 150 μm for 1989. At each main stream site, the net was held downstream of the operator and about 1 m^2 of substratum was thoroughly disturbed. At these sites the net was also moved in a sweeping motion to collect organisms in the water column. We were unsuccessful in devising a satisfactory quantitative method for sampling the dams. Peeled poplar sticks were placed in the dam, but by the next sampling date the sticks were gone, presumably moved by beavers. We used several qualitative techniques to sample the dams. If water was flowing over the dam's crest, the net was usually worked into the dam with the operator standing downstream. Then, wood and other material in the dam was thoroughly disturbed and the current carried specimens and debris into the net. When water was not going over the crest, a small part of the dam was taken apart, washing material into the net. These techniques were used for 5–10 min at several locations on each dam. In addition, woody material was removed from the dams and examined for specimens. In the field, organisms were preserved in 85% ethanol. In the laboratory, samples were washed through a series of sieves (8 cm, 4.0, 1.0, 0.6, and 0.4 mm), the sieved material was sorted, and organisms were identified at 7.5–30× magnification.

Data analysis

Cluster analysis and principal component analysis were used to determine trends in the macroinvertebrate data for each site and sampling date, normally 10 samples per date. For the cluster and principal component analysis, data were transformed ($\log x + 1$) to stabilize the variance and to obtain frequency distributions close to normality (Elliott 1977). The SAS/STAT statistical software package was used to perform the statistical analysis (SAS Institute Inc. 1988).

An agglomerative hierarchical cluster analysis determined groups of sites with similar taxonomic composition. Sites were grouped into clusters using Ward's minimum variance method, where two clusters combined at each step give the smallest increase of within-cluster variance. Principal component analysis summarized the data and identified characteristic taxa at the dam and main stream sites. This analysis transforms the original data matrix of sites by abundance of taxa to a matrix of sites by a smaller number of principal components (PC). Each PC is a linear transformation of the original data, represented by an eigenvector made up of coefficients (or weightings) for each taxon. Taxa that separate sites for each PC have high positive or negative eigenvector weightings. Principal component 1 (PC1) accounts for most of the total variation of taxa abundance, and subsequent PCs account for smaller amounts of variation. The first two or three PCs generally account for most of the variation. To determine if a PC separated the dam and main stream sites, sites were plotted on axes of PC1 × PC2 and PC1 × PC3.

Results

Faunal composition

The 1987 survey of 10 dams for two streams (North Fork and South Fork of the Bigoray River, including the two North Fork dams of the 1985–1987 study) indicated similar faunas for each of the 10 dams (Table 1). Fourteen taxa accounted for over 99% of the fauna at the two dams sampled routinely (dams 1 and 2), and 14 taxa accounted for over 97% of the fauna at the main stream sites (Tables 2 and 3). In part, this was due to the broad taxonomic categories used for certain taxa (by necessity, considering the large number of organisms that had to be processed). Seven taxa were abundant at both the dam and main stream sites. These were Simuliidae (Dip-

TABLE 1. Number of organisms of the 12 most abundant taxa collected from 10 dams, 11 June 1987, and the total number of organisms and total percent composition

	Dam number										All dams	
	North Fork							South Fork				
Taxon	1	2	3	4	5	6	7	8	9	10	Total no.	Total % composition
Simuliidae	860	4625	5496	205	3707	856	861	715	645	1457	19 427	72.35
Chironomidae	372	1716	356	487	1472	478	522	257	140	80	5 880	21.90
Baetis spp.	22	85	132	53	71	28	6	49	20	140	606	2.26
Nematoda	2	107	39	0	77	11	166	1	1	0	404	1.50
Dicranota spp.	4	27	11	5	9	13	9	21	6	1	104	0.39
Ilybius larvae	9	14	20	20	4	3	3	7	2	0	82	0.31
Pericoma sp.	0	2	7	0	35	16	2	13	1	0	76	0.28
Hydrachnidia	0	29	2	1	4	22	8	7	0	0	73	0.27
Limnephilidae	2	3	2	6	10	6	3	16	2	8	58	0.22
Caenis spp.	3	13	0	7	2	1	0	2	0	0	28	0.10
Amphinemura	0	12	0	0	0	1	0	6	1	0	20	0.07
Pisidium spp.	3	1	3	5	2	0	0	0	0	0	14	0.05
Others	3	11	7	7	8	13	7	11	8	4	79	0.30

NOTE: Dams No. 1 and 2 were the two dams routinely sampled during the 1985–1989 study.

TABLE 2. Total number of organisms and percent composition of the 14 most abundant taxa collected from the two dams, 1985, 1986, 1987

	Dam 1		Dam 2		Dams 1 and 2	
Taxon	No.	% composition	No.	% composition	Total no.	% composition
Simuliidae, L + P	45 333	86.60	16 832	67.03	62 165	80.26
Chironomidae, L + P	4 623	8.83	4 324	17.22	8 947	11.55
Amphinemura sp.	165	0.32	1 020	4.06	1 185	1.53
Hydropsyche spp.	34	0.06	843	3.36	877	1.13
Pericoma sp.	395	0.75	437	1.74	832	1.07
Baetis spp.	424	0.81	255	1.02	679	0.88
Dicranota spp.	201	0.38	311	1.24	512	0.66
Dytiscidae, A + L	42	0.08	343	1.37	385	0.50
Nematoda	245	0.47	74	0.29	319	0.41
Other Trichoptera	25	0.05	264	1.05	291	0.38
Hydrachnidia	128	0.24	55	0.22	183	0.24
Leptophlebia cupida	136	0.26	46	0.18	182	0.23
Limnephilidae	119	0.23	39	0.16	158	0.20
Pisidium spp.	85	0.16	44	0.18	129	0.17
Others	397	0.76	222	0.88	611	0.79

NOTE: A, adults; L, larvae; P, pupae.

tera), Chironomidae (Diptera), *Baetis* spp. (Ephemeroptera: Baetidae), *Pisidium* spp. (Pelecypoda: Sphaeriidae), Dytiscidae adults and larvae (Coleoptera), *Leptophlebia cupida* (Ephemeroptera: Leptophlebiidae), and Limnephilidae (Trichoptera) (Tables 1 and 2).

Although certain taxa were abundant at both the dam and main stream sites, faunal percent composition of the dams was strikingly different from that of the main stream sites. The dam fauna consisted of taxa usually associated with fast-flowing water, e.g., simuliids, certain chironomids, *Amphinemura* sp. (Plecoptera: Nemouridae), *Hydropsyche* spp. (Trichoptera: Hydropsychidae), and *Baetis* spp. (Table 2). Simuliidae larvae and pupae (almost all apparently of the *Simulium venustum/verecundum* complex) made up 80% of the dam macroinvertebrate fauna for the 1985–1987 data. Chironomids were the second most abundant taxa of the dams, and collectively simuliids and chironomids made up over 90% of the dam fauna. As indicated in the Methods, most of the 1985–1987 samples were taken in May, June, July, and August, and this influenced the total percent composition, because these were the months of large black fly populations. Had more samples been taken before May and after August, as was done in 1989 (see below), chironomids in the dams would have accounted for a larger proportion of the fauna (Fig. 1).

The main stream sites had a fauna more typical of slow-moving reaches of streams, e.g., certain chironomids, *Pisidium* spp., *Leptophlebia cupida, Caenis* spp. (Ephemeroptera: Caenidae), and cladocerans. Two taxa, Chironomidae and *Pisidium*, made up over 80% of the fauna at the main stream sites for the 1985–1987 data (Table 3). The chironomid fauna of the dams was different from the chironomid fauna of the main stream. The July 1988 chironomid fauna of the two dams consisted of 42% Tanytarsini, 39% Orthocladiinae, 18% Chironomini, and 1% Tanypodinae. The July 1988 sample of

TABLE 3. Total numbers of organisms and percent composition of the 14 most abundant taxa collected from the three main stream sites, 1985, 1986, 1987

Taxon	Main 1		Main 2		Main 3		Main 1, 2, and 3	
	No.	% composition	No.	% composition	No.	% composition	Total	% composition
Chironomidae, L + P	3578	42.64	8043	55.40	5812	46.01	17 433	48.67
Pisidium spp.	2768	32.98	4311	29.70	5145	40.73	12 224	34.13
Simuliidae, L + P	228	2.72	639	4.40	87	0.69	954	2.66
Naididae	521	6.21	154	1.06	216	1.71	891	2.49
Leptophlebia cupida	349	4.16	317	2.18	80	0.63	746	2.08
Cladocera	313	3.73	80	0.55	100	0.79	493	1.38
Caenis spp.	86	1.02	213	1.47	183	1.45	482	1.35
Corixidae	16	0.19	141	0.97	207	1.64	364	1.02
Ceratopogonidae	218	2.60	70	0.48	60	0.48	348	0.97
Limnephilidae	34	0.41	189	1.30	120	0.95	343	0.96
Sialis spp.	32	0.38	76	0.52	85	0.67	193	0.54
Physa spp.	2	0.02	66	0.45	100	0.79	168	0.47
Dytiscidae, A + L	17	0.20	63	0.43	56	0.44	136	0.38
Baetis spp.	48	0.57	43	0.30	41	0.32	132	0.37
Others	182	2.17	115	0.79	341	2.70	906	2.53

NOTE: A, adults; L, larvae; P, pupae.

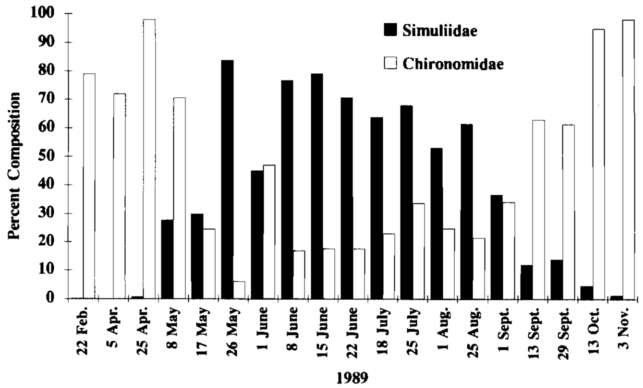

FIG. 1. Percent composition (as a fraction of total faunal composition) of Simuliidae and Chironomidae larvae and pupae, 22 February – 3 November 1989; data of dam 1 and 2 combined.

chironomids from the main stream sites consisted of 77% Tanytarsini, 10% Chironomini, 7% Tanypodinae, and 6% Orthocladiinae.

Chironomid larvae and pupae of the dams, considering the large number of species in this family, showed no discernible seasonality. In contrast, the dams' simuliid populations did exhibit seasonality, with large numbers of larvae first appearing in May and with continuing large populations through August (Fig. 1). By September, and apparently continuing through the winter, chironomids were the most abundant taxon of the dams (Fig. 1). Three unidentified simuliid larvae were collected in February, but none were collected in early April (Wiley 1991). Other studies of the *Simulium venustum/verecundum* complex in Alberta indicate that the population overwinters in the egg stage (Abdelnur 1968; Currie 1986).

Cluster analysis and principal component analysis

For the cluster and principal component analyses of the 1985–1987 data, organisms were grouped into 28 taxa to reduce the effect of taxa having sporadic occurrences (Table 4). Cluster analysis generally indicated separate clusters of dams (dams 1 and 2) and main stream sites (M1 through M4), except 3 October 1985, when there were three main clusters of sites (Fig. 2). For 15 sampling dates, all four dam sites (two sites at each dam) formed a cluster separate from main stream sites. For the remaining dates, all dam sites and one main stream site formed a cluster (on two dates), and three dam sites formed a cluster (on three dates) separate from other sites (Fig. 2). The two impounded sites of M1, although they clustered with the other main stream sites, usually clustered as units separate from the other main stream sites.

For 16 of 20 sampling dates, principal component one (PC1) separated the dam and main stream sites. As an example, the 25 June 1987 values are shown in Fig. 3. For three of the remaining dates, PC1 separated three of the four dam sites from the other sites. Principal component one indicated different groups of taxa at dam and main stream sites, and these taxa were usually the same for each of the 3 years (Table 4). The second and third PCs did not separate all dam sites from main stream sites for any sample dates (e.g., Fig. 3). Principal component one accounted for a mean of 39% (range = 28–52%) of the total variation in the abundance of taxa, while PC2 and PC3 accounted for 18 and 13% of the total variance, respectively.

Discussion

Faunal composition

The results show different macroinvertebrate assemblages on beaver dam substrata compared with main stream sites. A major feature of the beaver dam fauna was the large proportion of simuliid larvae compared with main stream sites of this stream and with areas of other studies of beaver-altered streams. For example, in an extensive survey of beaver-altered streams of Quebec, Canada, Naiman et al. (1984) found simuliids making up only a small part of the annual biomass, with no significant differences in simuliids between riffles and beaver-altered areas. In our study during the summer, simuliid larvae and pupae made up 80% of the fauna of dams, and they occurred in large numbers. For example, the number of individual simuliid larvae and pupae collected, using the 150-μm-mesh net, from the two dams in June 1989 (Fig. 1) was 19 320

TABLE 4. Summary of principal component 1 results

Site/ taxonomic group	Number of sampling dates with the greatest eigenvector coefficients: 1985	1986	1987	1985–1987
Dam sites				
Tipulidae	4	6	7	17
Simuliidae	5	6	4	15
Plecoptera	4	4	4	12
Hydropsychidae*	3	3	4	10
Psychodidae	3	0	6	9
Other Coleoptera	0	4	2	6
Baetidae	1	3	2	6
Hydrachnidia*	0	2	3	5
Nematoda	1	3	1	5
Leptophlebiidae*	1	2	0	3
Corixidae*	1	1	0	2
Dytiscidae*	0	1	1	2
Other Diptera*	1	1	0	2
Anisoptera*	0	2	0	2
Other Trichoptera*	0	1	0	1
Cladocera*	0	0	1	1
Limnephilidae*	0	1	0	1
Oligochaeta*	1	0	0	1
Main stream sites				
Sphaeriidae	3	8	7	18
Sialis spp.	2	6	5	13
Caenis spp.	1	5	3	9
Hirudinea	3	2	3	8
Chironomidae	1	3	3	7
Oligochaeta*	1	4	2	7
Corixidae*	1	3	2	6
Leptophlebiidae*	1	2	2	5
Gastropoda	2	0	1	3
Anisoptera*	2	0	1	3
Ceratopogonidae	0	2	1	3
Cladocera*	2	0	1	3
Other Ephemeroptera	2	0	1	3
Other Trichoptera*	0	1	1	2
Hydrachnidia*	1	0	1	2
*Hyalella azteca**	1	1	0	2
Limnephilidae*	0	1	1	2
Other Diptera*	0	1	0	1
Hydropsychidae*	0	1	0	1
Dytiscidae*	1	0	0	1
Ephemera simulans	1	0	0	1

NOTE: Data indicate taxonomic groups with the greatest eigenvector coefficients at the dams and main stream sites for all sampling dates in each year and for 1985–1987 combined. Five taxonomic groups with the greatest positive and negative eigenvector coefficients were used for each sampling date.

*Groups occurring at both the dam and main stream sites.

(1 June), 32 928 (8 June), 19 776 (15 June), and 29 360 (22 June). Beaver dams appear to be major sources of these economically important biting flies in slow-moving boreal streams. Both simuliids and chironomids can complete their life cycle on the substratum of the dams, as indicated by large numbers of simuliid and chironomid pupae at the dams.

In autumn, winter, and early spring, chironomids were the most important component of the dams' fauna; at this time the major blackfly species, the *Simulium venustum/verecundum* complex, was in the egg stage. McDowell and Naiman (1986), for a Quebec, Canada, stream altered by beavers, separated their study area into two riffles, a reach (representing a low gradient site), and a beaver pond. They found Orthocladiinae abundant at all sites, Tanytarsini only abundant in riffles, and Chironomini and Tanypodinae replacing Tanytarsini as the dominant chironomids of the beaver ponds. The chironomid composition in our study, determined from one date in July, indicates that Tanytarsini was the dominant group at the main streat sites, whereas both Tanytarsini and Orthocladiinae were abundant at the dams.

Collectively, simuliid and chironomid larvae and pupae made up over 90% of the dam fauna, but other taxa also occurred in substantial numbers although, because of the large numbers of simuliids and chironomids, their percent composition is not impressive. The fauna of the dams was typical of a fast-flowing habitat, whereas animals of the main stream sites were more characteristic of slow-flowing or lentic habitats. Cluster analysis separated the dam and main stream sites for each sampling date and year based on composition of the macroinvertebrate community. And examination of taxonomic groups at all sites, using both faunal percent composition and principal component analysis, revealed that many taxa were dominant either at the dams or the main stream sites for each year of the study.

Functional feeding groups

The dominant taxa of the dams and their functional feeding categories (using the classification scheme of Merritt and Cummins (1984)), in addition to filter-feeding simuliid larvae and chironomid larvae (with diverse functional feeding categories), included *Hydropsyche* larvae (filter feeders), *Amphinemura* nymphs (shredders), *Pericoma* larvae and *Baetis* nymphs (collector gatherers and scrapers), and *Dicranota* (Diptera: Tipulidae) and Dytiscidae, especially *Ilybius*, larvae (predators). Most common taxa of the main stream sites, in addition to chironomids, included filter feeders (*Pisidium*, Cladocera), collector gatherers and scrapers (Naididae (Oligochaeta), *Leptophlebia cupida, Caenis*) and predators (*Sialis* (Megaloptera), Corixidae (Hemiptera), Hirudinea). Although the invertebrate assemblages of the dams differed from those of the main stream sites, both habitats included similar functional feeding groups, except for a shredder (*Amphinemura*), found only at the dams. McDowell and Naiman (1986), in their study of a beaver-altered stream, found an abundance of filterers both in impounded sites and in riffles of the stream. They also found scrapers more abundant in riffles, whereas predators were more abundant in impounded sites.

The beaver dam compared with similar habitats

It would be instructive to compare the fauna of our dams with the fauna of beaver dams of streams in different geographical areas. But we know of no other studies of invertebrates of beaver dam substrata. Smock et al. (1989) studied macroinvertebrates of debris dams in low-gradient headwater streams in Virginia, U.S.A. These debris dams (each dam being small enough to be completely removed as a sample) in some respects resemble minute beaver dams. They manipulated debris dams and found that increasing the abundance of the debris dams increased macroinvertebrate abundance and increased the importance of shredders in the biomass. Woody snags (e.g., submerged tree trunks and branches) are another habitat with similarities to beaver dams. Benke et al. (1984) found a much greater diversity of invertebrate taxa on snags than in sandy or muddy areas of a blackwater subtropical river. At the ordinal level, the taxa of the snags are compar-

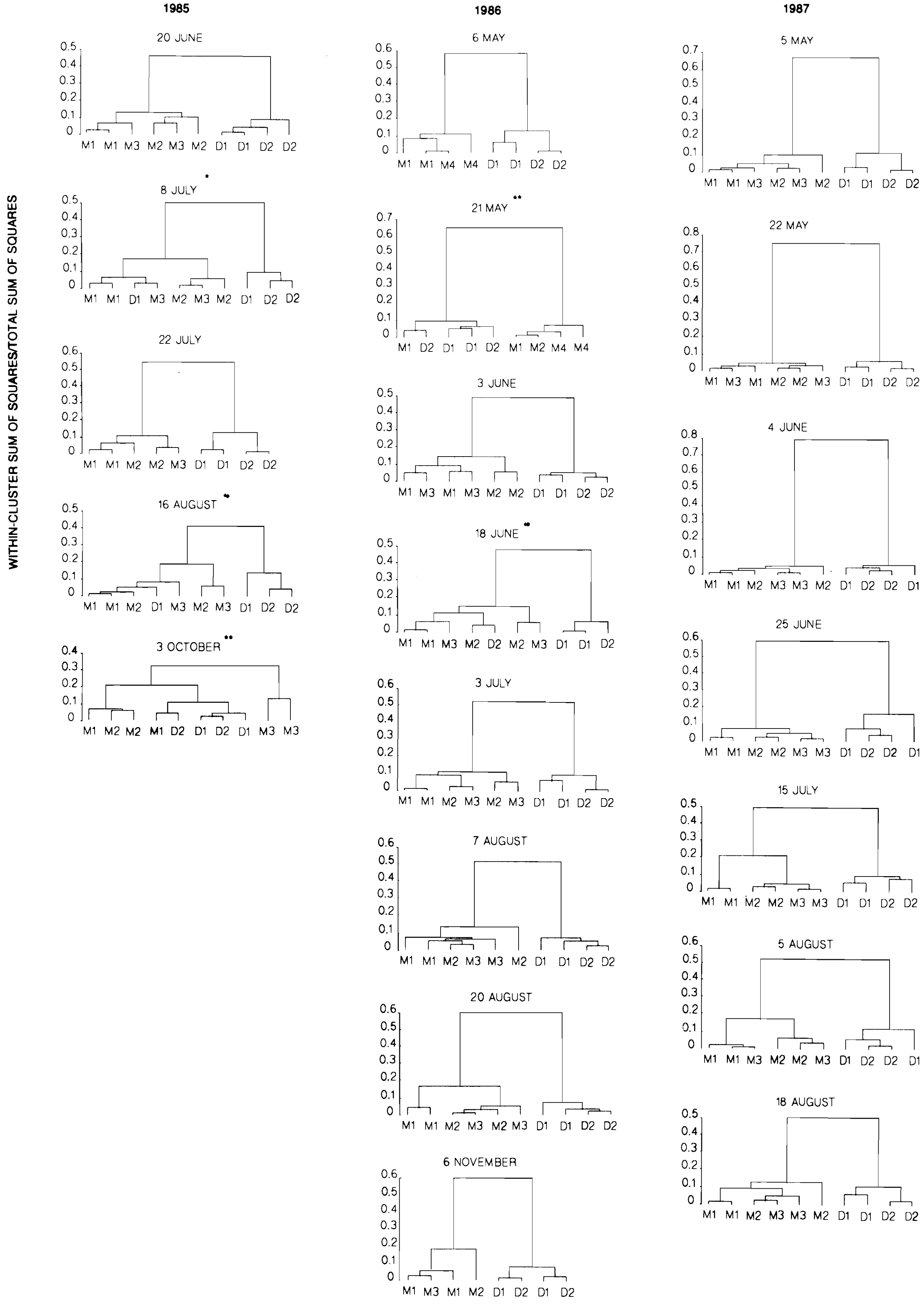

FIG. 2. Dendrograms showing clusters of dam (D) and main stream (M) sites for each sampling date, 1985, 1986, 1987, based on Ward's minimum variance method. Within-cluster variance is expressed as a proportion of the variance. Asterisks indicate a cluster of three dam sites (*) or four dam and one main stream site (**) separated from other sites.

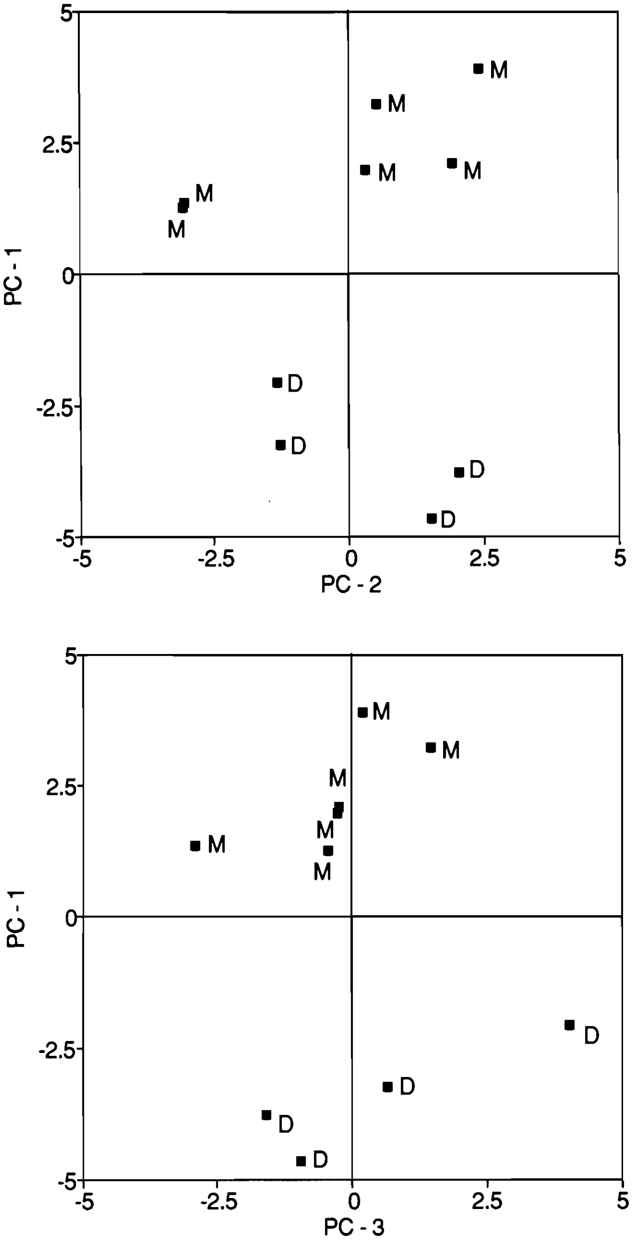

FIG. 3. Dam (D) and main stream (M) sites plotted on axes of principal component 1 (PC1) × PC2 and PC1 × PC3; 25 June 1987.

able to what we found at beaver dams. Benke et al. (1984) found filter-feeding trichopterans (mainly *Hydropsyche* spp.), simuliids (*Simulium* spp.), and chironomids (with diverse feeding strategies) to be the major consumers on snags. They calculated production for the abundant taxa and observed that the small amount of habitat represented by the snags was contributing a significant amount of total biomass to this blackwater stream. We did not make production estimates for the beaver dam taxa, but are convinced that woody beaver dams, like woody snags, are more important as habitats for invertebrates than indicated by the small areas of these structures relative to the substratum area of the stream channel generally.

Beaver dams might also be compared with lake outlets. Many workers have found large populations of blackflies at impounded outlets and for short distances downstream (e.g., Spence and Hynes 1971; Carlsson et al. 1977; Sheldon and Oswood 1977; Colbo and Porter 1979; Lake and Burger 1983). Wotton (1992) discusses communities of filter feeders at surface-release lake outlets and points out that a disadvantage for these filter feeders is the possibility of the impoundment's water level dropping to the point where water ceases to flow over the spillway or crest of the dam, and thus dries up the habitat of the lake outlet taxa. In our study, during low water, water often ceased flowing over the dam's crest, but this appears to be less disastrous for the beaver dam's filter feeders than what Wotton (1992) described for artificial lake outlets. Water continuously flowed through the beaver dam even when water was going over the crest. And when water stopped flowing over the dam, filter feeders utilizing water flowing through the dam maintained populations at the dam. Also, simuliids, chironomids, and trichopteran larvae filter feeding at the crest would have relatively short distances to move to find flowing water and in this way would possibly survive drops in the beaver dam's water levels.

Richardson and Mackay (1991) reviewed studies and assessed factors that might account for dense assemblages of filter feeders at lake outlets. The beaver dam is usually a much smaller area than that included in studies of lake outlets, which Richardson and Mackay define as including the dam (natural or man-made) and the outflow stream "to some point downstream where the effects of the lake are no longer detectable." Also, the substratum of beaver dams, with the large woody component, is often of a different kind than the substrata of natural and artificial lake outlet areas. Nevertheless, the beaver dam's fauna is probably responding to events and factors consistent with events and hypotheses considered by Richardson and Mackay for lake outlets. The hypotheses they assessed to account for large assemblages of filter feeders at lake outlets dealt with food, temperature, flow regime, substratum, competition, predation, and the colonization cycle. All these hypotheses could be pertinent in structuring the fauna (filter feeding and not filter feeding) of beaver dams. Richardson and Mackay conclude that, although the hypotheses are not always independent, hypotheses involving food, depth of water, competition, and the colonization cycle have the strongest empirical support. They suggest that certain taxa of filter feeders, especially some simuliids, are outlet specialists.

We propose that the physical presence of the barrier extending entirely across the stream channel, and flow, are major factors accounting for the initial establishment of large populations of simuliid larvae and other lotic taxa at beaver dams. The substrata of the dam would intercept most of the water and therefore many of the organisms moving downstream in the water column. The dam probably acts as a net, catching drifting invertebrates and also trapping large amounts of allochthonous material, which further increases the diversity of habitats and food at the dam. Different sizes and shapes of woody substratum oriented in numerous ways relative to water flowing over and through the dam would create a wide array of current velocities at the dam. This would enhance the possibility of simuliid larvae finding an area of optimum flow for filter feeding someplace in the dam (Ciborowski and Craig 1989). More specifically, these areas would provide flow with high Froude numbers (the ratio of gravitational forces; Newbury 1984) now known to be important for habitat choice by simuliid and trichopteran larvae (Statzner 1981; Craig and Galloway 1988; Wetmore et al. 1990). The result would be a habitat suitable for lotic invertebrates in a stream with otherwise few typically lotic regions. The texture of the woody substratum could also be important. Clifford et al. (1992) found more simuliid larvae colonizing smooth tiles than rough tiles, even though after the 14-day colonization period there were few simuliid larvae on tiles of either texture.

Numerous beaver dams, such as are now found in the Bigoray River, appear to concentrate large black fly populations in small areas, namely, the dams. Our contention is not that beaver dams necessarily increase black fly populations in streams. They may, but we cannot conclude this from our data, since our study was not designed to assess faunal composition changes before and after extensive alterations by beavers. Benthic data are available prior to beaver populations increasing noticeably in the drainage, but were done in a riffle and in pools of the main stream not created by beavers. Although some beaver dams were present in the area at that time, they were not sampled. A 1966–1967 study (Clifford 1969) indicated that black fly larvae made up 5% of the total benthic fauna in the main stream. A synthesis of studies carried out between 1966 and 1976 (Clifford 1978) indicated that black fly larvae accounted for 4% of the Bigoray River fauna in the main stream.

Our study indicates that the dams play an important role in supporting large populations of simuliids and generally in maintaining a lotic fauna in these slow-moving, low-gradient boreal streams with numerous beaver impoundments. We suggest that beaver dams represent a habitat more important than indicated by the relatively small areas encompassed by these barriers. Beaver dams should be considered important sampling areas in future studies of beaver-altered systems.

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