

## Original papers

# Structure and function of a benthic invertebrate stream community as influenced by beaver (*Castor canadensis*)

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**Summary.** Beaver (*Castor canadensis*) affect the benthic invertebrate community of small woodland streams in Quebec through habitat modifications. Their activities influence community structure through the replacement of lotic taxa by lentic forms and community function by increasing the absolute importance of collectors and predators while decreasing the relative importance of shredders and scrapers in impounded sites. At our study site during the 1983 ice-free season, standing stocks of coarse particulate organic matter (>1 mm) were 2–5 times greater ( $P < 0.05$ ) in impounded sites than riffle sites in spring and summer. Fine (212  $\mu\text{m}$ –1 mm) and very fine (0.5  $\mu\text{m}$ –212  $\mu\text{m}$ ) particulate organic matter were 3–10 times greater ( $P < 0.05$ ) in impounded sites in all seasons. Chlorophyll *a* standing stocks did not differ statistically among sites. Total density and biomass of invertebrates in impoundments were 2–5 times greater ( $P < 0.05$ ) than riffle sites in spring and summer, but statistically similar in autumn. Generic diversity ( $H'$ ) was greater ( $P < 0.05$ ) in unaltered sites in autumn. Non-impounded sites were dominated by Simuliidae, Tanytarsini chironomids, scraping mayflies and net spinning caddisflies while impounded sites were characterized by Tanyptodinae and Chironomini chironomids, predacious odonates, Tubificidae, and filtering polychaetes. Our results suggest that current paradigms applied to lotic ecosystems need to be reevaluated to incorporate the influence of beaver upon invertebrate communities.

The success of these models rests, in part, upon their ability to incorporate natural alterations into a theoretical framework. Beaver (*Castor canadensis*) may represent an important, however as yet ignored (but see Naiman et al. 1985), component of lotic paradigms as natural “modifiers” of lotic ecosystems.

Recent proposals suggest that beaver have a substantial influence upon the structure and function of low order streams through the alteration of channel geomorphology by dam construction and wood inputs (Naiman et al. 1985). These effects include retention of sediment, organic matter and water within impoundments, an increase in stream surface area, and modifications to nutrient cycling, decomposition dynamics and the riparian zone (Hodkinson 1975a, b; Naiman and Melillo 1984; Naiman et al. 1985). Habitat alterations may result in modifications of ecosystem parameters in which properties typically associated with lower order streams (eg. high detrital standing stock) or higher order streams (eg. high adult insect production) are observed in impounded sites. Ecosystem parameters possibly unique to beaver ponds (eg. susceptibility to disturbance, i.e. drought or floods), have also been suggested (Naiman et al. 1985).

The effect of beaver on invertebrate community structure and function has received little attention. Descriptive and energetic studies have documented the emergence of adult insects from beaver impoundments. These investigations have revealed that adult assemblages in impounded sites differ from temporally (Sprules 1940) and spatially (Hodkinson 1975a; Naiman et al. 1984) separated non-impounded sites. However, no studies are reported that elucidate the influence of beaver on the structure and function of benthic, in situ, invertebrate communities.

This study reports how recent beaver activity has affected the benthic invertebrate community of a small woodland stream in north-eastern Quebec. Results are presented in relation to the interaction between beaver induced environmental modifications and the structure and function of lotic benthic communities.

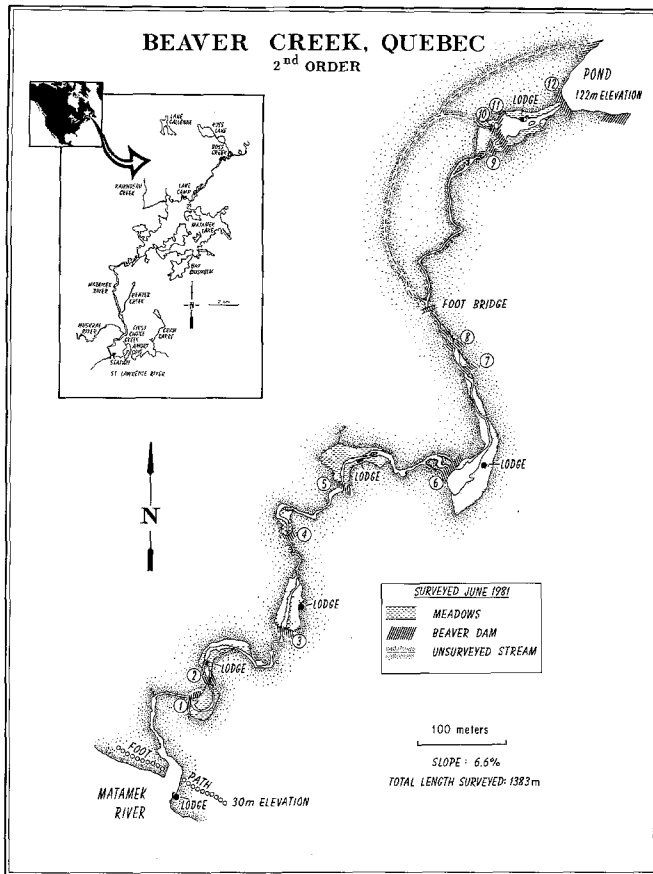
### Site description

Beaver Creek is situated on the north shore of the Gulf of St. Lawrence in north-eastern Quebec, within the Matahek River watershed (Fig. 1). A detailed description of the stream has been given by Naiman (1983) and Naiman and Melillo (1984). The stream lies on the Precambrian Shield

The development of ecological theory and use of experimentation in lotic habitats has been, in large part, concerned with describing and understanding benthic invertebrate communities (see Barnes and Minshall 1983). This includes variation in the structure and function of benthic communities in streams of differing size (Vannote et al. 1980; Minshall et al. 1985a, b; Statzner and Higler 1985), with different disturbance regimes (Ward and Stanford 1983; Reice 1985) and with differing sediment characteristics (Rabeni and Minshall 1977; Minshall and Minshall 1977; Reice 1980; Culp et al. 1983; Culp and Davies 1985). These models implicitly incorporate the effects of natural alterations of lotic habitats upon community structure and function.

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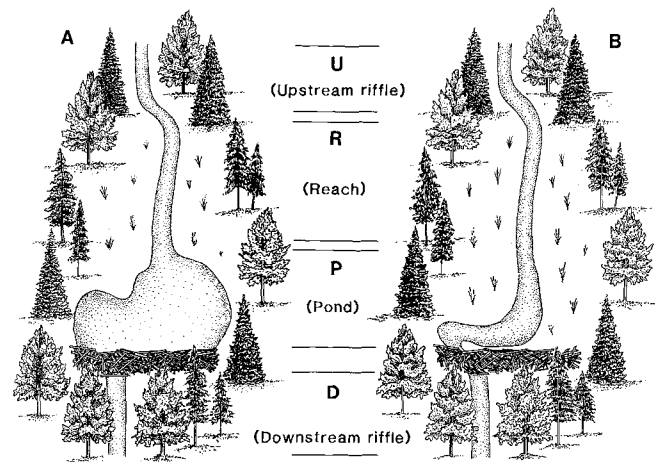


**Fig. 1.** Map showing the location of the Matamek River watershed and the study site. Sampling was confined to sites above and below dam No. 3

in a subarctic climate (mean annual temperature  $1^{\circ}\text{C}$ ). Streams in this area are typically brown water, low nutrient ( $<0.3\text{ mg N/L}$  as nitrate and  $<0.003\text{ mg P/L}$  as orthophosphate) and slightly acidic (pH: 4.8–7.2). The dominant tree species are black spruce (*Picea mariana*) and balsam fir (*Abies balsamea*). Streamside vegetation is predominantly paper birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), speckled alder (*Alnus rugosa*) and willow (*Salix* sp.).

Beaver Creek is a 1.4 km, second order stream (catchment area  $1.83\text{ km}^2$ ), comprised of a series of 12 inactive beaver dams, separated by high gradient riffles. Before the study no permanent beaver activity had been observed at the study area for several years. Benthic samples were collected above and below dam No. 3 (Fig. 1), which has been uninhabited for  $\sim 8$  years. During high discharge (spring and fall) the water level rises 0.5 m creating a large pond (Fig. 2a). During low flow the pond reverts to a low gradient meander (Fig. 2b). The dam immediately upstream (No. 4, Fig. 1) was destroyed several years prior to this study. Any immediate effect of previous beaver activities from upstream is believed negligible due to the distance ( $\sim 300\text{ m}$ ) from the study area.

The study area was subdivided into 4 discrete sites (Fig. 2, Table 1). The upstream riffle (U) ( $\sim 100\text{ m}$  from the dam) is a high gradient site ( $\sim 5\%$ ) with nearly complete canopy cover (70–90%). The substrate is composed of large boulders, gravel and sand. The reach (R) is a low gradient



**Fig. 2A, B.** Graphical representation of the study area illustrating the location of the four sites; U upstream riffle, R reach, P pond, D downstream riffle. A Channel morphology during high flow (spring and autumn); B during low flow (summer)

**Table 1.** Description of physical characteristics associated with each of the sampling sites on Beaver Creek. Quantitative data are given as the range of values encountered

Parameter	Upstream riffle	Meadows (reach)	Beaver Pond	Down stream riffle
Substrate	boulders, sand	sand, silt, wood, detritus	silt, wood, detritus	boulders, gravel
Riparian vegetation	alder, fir, aspen, spruce	grasses	grasses	alder, fir, aspen, spruce
Canopy	moderate-closed	open	open	closed
Bank slope	steep-moderate	flat	moderate-flat	moderate
<b>Spring</b>				
Depth (cm)	16–21	6–14	13–24	17–24
Width (m)	1–4	1–2	10–15	1–2
Velocity (m/sec)	0.33–0.50	0.07–0.29	0.01–0.03	0.36–1.43
Temperature ( $^{\circ}\text{C}$ )	13–12	12–11	10	10
<b>Summer</b>				
Depth (cm)	10–18	7–11.5	7–16	6–21.5
Width (m)	1–3	1	2–3	1
Velocity (m/sec)	0.25–0.28	0.28–0.36	0.01–0.05	0.20–0.59
Temperature ( $^{\circ}\text{C}$ )	14	13	13	13
<b>Autumn</b>				
Depth (cm)	20–23	19–30	30–47	17–21
Width (m)	1–4	1–2	10–15	1
Velocity (m/sec)	0.22–0.54	0.24–0.33	0.05–0.10	0.39–0.63
Temperature ( $^{\circ}\text{C}$ )	6	6	6	6

site (<1%) bordered by sedge meadows. Sediments are silt, sand and wood (10–20 kg/m<sup>2</sup>). The reach and adjacent meadows exemplify the intermediate successional stages of a receding pond. The beaver pond (P) is characterized by thick (>0.5 m), fine sediments, a large quantity of wood (>40 kg/m<sup>2</sup>) and little canopy (0–10%). The final site (D), below the dam, is a high gradient riffle (8–10%) similar to the upstream riffle except for a more complete canopy (90–100%) and greater water velocities.

### Materials and methods

Three sets ( $n_i = 12$ ) of seasonal benthic samples were collected in 1983 during the ice-free period. Collections were made of June 2 (spring), July 21 (summer) and October 7 (autumn). For each sample, measurements of water depth, channel width, water velocity (estimated with rhodamine dye by recording the time to travel a predetermined distance) and water temperature were obtained.

Benthic samples were collected using a 10 L bottomless bucket (surface area = 0.045 m<sup>2</sup>). The bucket was pushed into the substrate, encircled by sand bags and the contents (sediment and benthos) removed to a depth of 10 cm. The bucket was emptied in 15–30 s. If water seepage occurred, the bucket was sampled continuously (3–4 min) until all the contents were removed. The sample was diluted to a final volume of 20 L. After agitation, three 250 ml subsamples were obtained to estimate very fine particulate organic matter (VPOM, details below). The remaining sample was fixed in 70% ethanol after rinsing through a 212  $\mu$ m sieve. At each sample location a portion of nearby (<0.25 m distant) surface substrate (riffle sites: small boulders, cobbles and wood; impounded sites: 200 ml of sediment (sand, silt and detritus) and wood) was obtained for chlorophyll determination.

Standing stock of chlorophyll *a* was estimated using the method of Lorenzen (1967). Chlorophyll *a* was extracted with 100% acetone (final concentration of ~90%). Spectrophotometer readings were made after 24 h. Chlorophyll, corrected for phaeophyton, was expressed as mg/m<sup>2</sup> by obtaining the surface area of rocks and wood (Naiman 1983; Bott et al. 1985) or for sediments, by relating the mass of sediment used to a known mass per m<sup>2</sup> for each sample location.

Particulate organic matter was separated into three size fractions: coarse particulate organic matter (CPOM), >1 mm diameter, fine particulate organic matter (FPOM), 1 mm–212  $\mu$ m and VPOM, 212  $\mu$ m–0.5  $\mu$ m. Each sample was dried at 60° C for 24 h (after removal of invertebrates) and a subsample ashed at 450° C for 3 h to obtain ash free dry mass (AFDM).

Invertebrates (stained with rose bengal) were removed from all size fractions and identified to the lowest possible taxonomic level (generally genus; chironomids to tribe or subfamily), dependent upon available keys. Twenty-eight of the 108 possible samples (25.9%), were split by 1/2 or 1/4 and those portions examined for invertebrates. On 7 of 108 occasions (6.5%) 1/8 of the sample was examined; all were FPOM fractions. A group of representative individuals from each identified taxon, of each sample, were dried at 60° C for 24 h, and biomass obtained on a Cahn electrobalance. Each taxon was categorized by functional feeding group (Cummins 1973; Cummins and Klug 1979) as described by Merritt and Cummins (1984). Several groups

(most notably the Orthocladiinae) are diverse and could not be categorized. Whitley (1982) and Pennak (1978) provided descriptions for oligochaetes and pelycopods, respectively.

In addition to describing each taxon or trophic group by density and biomass a third response variable, Importance Value (IV), was calculated as:

$$IV = (B_i + D_i)/2.$$

where  $B_i$  is the proportional biomass of taxon or trophic group *i*, and  $D_i$  is the proportional density of taxon or trophic group *i* within a sample.

Diversity indices (generic) for each sample were determined. The Shannon-Weaver Index ( $H'$ ), generic evenness ( $J$ ) and generic richness ( $S$ ) were obtained with density data (Pielou 1977).

Tests for significant differences in the mean seasonal values of chlorophyll, CPOM, FPOM, VPOM, total density and total biomass among sites were made with a one-way parametric ANOVA (SAS version 82.3) with sites treated as fixed effects. Seasons were not considered as a factor in the design. Homogeneity of variance was tested by the  $F_{\max}$  test (Sokal and Rohlf 1981). Transformations,  $\ln(x+1)$ , to stabilize variances were used when necessary. The Student-Newman-Keuls test was used as an *a posteriori* test to observe differences among treatments when the overall ANOVA was significant (Type I error = 5%). In testing differences within trophic groups among sites, the data were treated as a multivariate design. A nonparametric Kruskal-Wallis test was used to test for differences in  $H'$ ,  $J$  and  $S$  between sites to avoid distributional assumptions (Sokal and Rohlf 1981). A cluster analysis (SAS version 82.3) was used to assess similarity in species assemblages using IV data for each taxon.

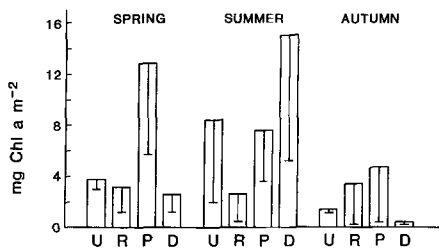
### Results and discussion

#### *Environmental variables*

**Physical parameters.** Physical characteristics associated with each of the sites were seasonal (Table 1). Water depth and channel width fluctuated little in riffle sites, while impounded sites decreased in depth and width during summer. Water velocity was greatest at downstream riffle sites. In summer and autumn the upstream riffle and reach sites had similar water velocities, while in spring the upstream riffle had greater velocities. Velocities were least in the pond in all seasons. Water temperatures were similar in spring and summer, yet appreciably lower in autumn.

**Chlorophyll.** There was no significant difference in the standing stock of chlorophyll among sites in any season (Fig. 3: spring  $P=0.15$ ; summer  $P=0.47$ ; autumn  $P=0.83$ ). The large variability is attributable to the patchiness of algae and moss in riffles, and the overestimation of chlorophyll in sediments by its extraction from detritus. The mean values reported here are greater (~100–200%) than those given by Naiman (1983) for the same stream. However, determinations made for adjacent streams during 1983 (Reice and Naiman 1986) are also greater (~100%) than previously reported for these streams (Naiman 1983).

**Detrital standing stock.** Standing stock of CPOM was significantly greater (2–5 times) in beaver altered sites in both



**Fig. 3.** Standing stocks of chlorophyll *a* at each site and season. Site designations are as in Fig. 2. Error bars are 1 S.E. Means are for 3 replicates except in autumn for U and R when  $n=2$

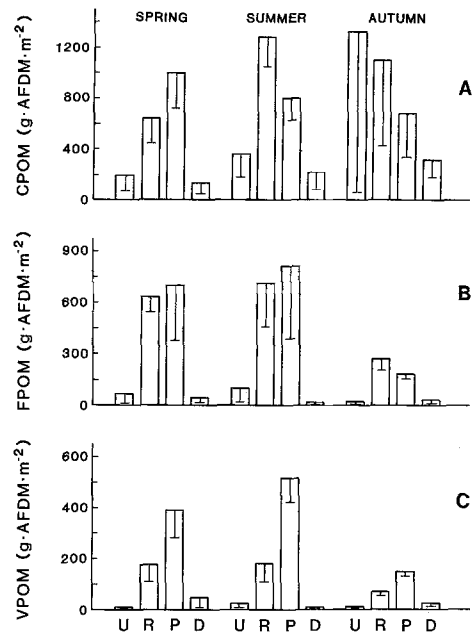
spring ( $P=0.03$ ) and summer ( $P=0.01$ ; Fig. 4a). In spring the pond ( $\bar{x}=997$  g AFDM/m<sup>2</sup>) and reach ( $\bar{x}=623$  g AFDM/m<sup>2</sup>) sites were statistically similar, while in summer CPOM in the reach ( $\bar{x}=1,268$  g AFDM/m<sup>2</sup>) was significantly greater than in the pond ( $\bar{x}=672$  g AFDM/m<sup>2</sup>). No significant difference in CPOM was observed between sites in autumn ( $P=0.75$ ). Autumn samples were obtained following peak leaf fall. One would expect the distribution of CPOM to be uniform since little physical movement or biological fragmentation would have yet occurred.

Standing stocks of FPOM and VPOM were significantly different across sites during all seasons (Fig. 4b: spring  $P=0.02$ ; summer  $P<0.01$ ; autumn  $P<0.01$ ; Fig. 4c: spring  $P=0.03$ ; summer  $P<0.01$ ; autumn  $P<0.01$ ). FPOM was significantly greater (7–10 times) in the reach and pond in all seasons; these sites did not differ from each other. In each season, VPOM was significantly more abundant (>100%) in the pond than the reach which, in turn, was greater (3–6 times) than either riffle site. The riffle sites did not differ significantly from each other.

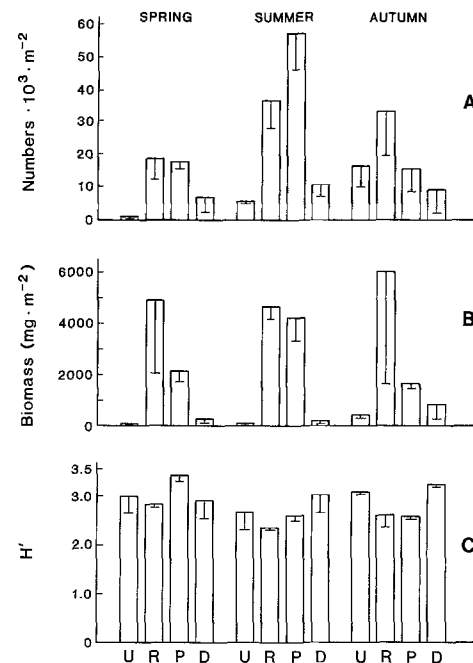
Hodkinson (1975a) reported a high standing stock of organic matter and decreased particle size of sediments in beaver altered sites relative to adjacent non-impounded sites. Naiman et al. (1985) have reported CPOM and FPOM standing stocks often 1 to 3 orders of magnitude greater in beaver impounded areas than nearby riffle sites. Impoundments may be quite old (i.e. > 50 years) and the retention of detritus can be substantial. The occurrence of FPOM and VPOM at high concentrations in impounded sites is expected since these size fractions settle out where water velocities are greatly reduced. This material may also be highly refractory (Bird and Kaushik 1981; Hodkinson 1975b) and persist for long periods under anaerobic conditions if flooding is unable to move deposits.

#### Invertebrate community

**Density.** Total mean density of invertebrates was significantly greater in beaver impounded sites during spring ( $P=0.04$ ) and summer ( $P<0.01$ ; Fig. 5a). Mean densities in the reach and pond were statistically similar (range: spring 11,052–30,283/m<sup>2</sup>; summer 24,005–72,724/m<sup>2</sup>) but greater ( $P<0.05$ ) than either riffle (range: spring, 596–11,251/m<sup>2</sup>; summer, 3,492–12,467/m<sup>2</sup>). In autumn no significant difference ( $P=0.22$ ) between sites was observed (range:  $D=928$ /m<sup>2</sup>;  $R=58,356$ /m<sup>2</sup>). Densities reached a maximum ( $\bar{x}=55,600$ /m<sup>2</sup>) during summer in the beaver pond. These high densities are perhaps the result of; a) low water discharge, concentrating individuals into a smaller wetted area, b) a consequence of a large number of early instar larvae result-



**Fig. 4A–C.** Standing stocks of detritus at each site and season. Site designations are as in Fig. 2. Error bars are 1 S.E. **A** CPOM, **B** FPOM, **C** VPOM



**Fig. 5A.** Total density of invertebrates at each site in each season. **B** Total standing biomass of invertebrates at each site in each season. **C** Generic diversity (Shannon-Weaver). Site designations are as in Fig. 2. Error bars are 1 S.E.

ing from the peak emergence of adults in early June (Naiman et al. 1984), or c) habitat characteristics (see below).

**Biomass.** Total mean biomass of invertebrates was also significantly greater during spring ( $P<0.01$ ) and summer ( $P<0.01$ ) in beaver impounded sites (Fig. 5b; range: spring 1.341–11.130 g/m<sup>2</sup>; summer 2.738–5.098 g/m<sup>2</sup>) than riffle

sites (range: spring 0.071–0.558 g/m<sup>2</sup>; summer 0.078–0.379 g/m<sup>2</sup>), yet was similar across sites in autumn ( $P=0.22$ ; range:  $D=0.040$  g/m<sup>2</sup>;  $R=13.573$  g/m<sup>2</sup>). Total mean biomass and total mean density were positively correlated ( $r=0.77$ ,  $P<0.05$ ) across samples ( $n=36$ ).

Egglshaw (1964) and Culp and Davies (1985) have shown a positive correlation between the density of colonizing invertebrates and the standing stock of detritus. Hodkinson (1975a) suggested particle size, organic matter content and C/N ratio of the sediments influenced the composition of emerging adults from beaver impoundments. However, Culp et al. (1983) and Culp and Davies (1985) have demonstrated detrital standing stocks may be more important than particle size in determining the relative abundance of many lotic invertebrates. Results reported here also support these contentions. Stepwise linear regressions of invertebrate density and biomass in each season upon standing stocks of detritus (i.e. CPOM, FPOM, VPOM) resulted in significant ( $P<0.05$ ) models in spring and summer (Table 2). Regression coefficients were positive in all models suggesting increased standing stocks of detritus result in greater densities and biomass of invertebrates. The best predictor of density and biomass in spring and summer was FPOM. CPOM was an important component of the models only in autumn.

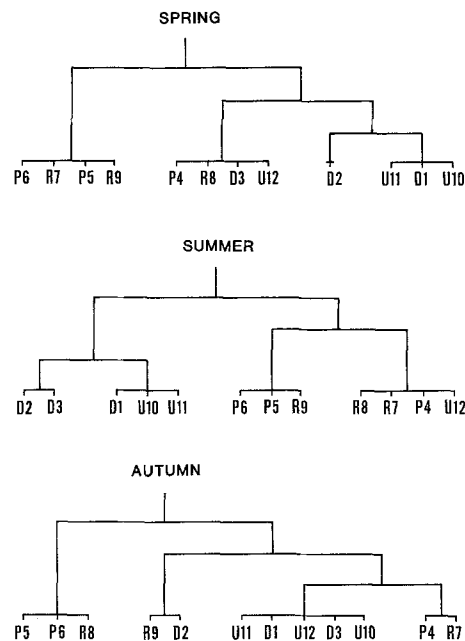
**Diversity indices.** A total of 75 taxa were identified across all sites. Generic diversity ( $H'$ ), was significantly different between sites in autumn only (Fig. 5c;  $P=0.03$ ). Greatest diversities were in riffle sites ( $U$ ;  $H'=3.00$ ,  $D$ ;  $H'=3.17$ ); impounded sites significantly less ( $R$ ;  $H'=2.63$ ,  $P$ ;  $H'=2.60$ ). Generic richness ( $S$ ) differed significantly between sites in summer ( $P=0.04$ ;  $P:S=19$ ;  $D:S=20$ ;  $U:S=12$ ;  $R:S=13$ ). Equitability ( $J$ ) was not different ( $P>0.05$ ) among sites in any season. These data are underestimates of the true generic diversity, due to the exclusion of chironomid genera. However, these estimates should reflect relative trends between sites.

**Faunal associations.** The analysis of similarity between faunal assemblages indicates strongly two distinct community types (Fig. 6; 4 clusters were produced reflecting original number of sites). In general assemblages from high gradient (riffle) or low gradient (pond and reach) sites were more similar within than between sites. Twenty-six of 36 assemblages (72.2%) were clustered with only similar sites, while 4 of 36 (<12%) were clustered with differing sites. These four include; a) in spring the riffle site (D3) immediately below (<0.1 m) the dam and the furthest upstream riffle site (U12) which were both clustered with low gradient sites; b) in summer U12 clustered with low gradient sites and c) in autumn the reach site (R9) closest the upstream riffle (<5 m), grouped with a riffle site.

The dominant fauna for each site were defined by including those taxa with IV's greater than 10% (Table 3). Non-impounded sites were dominated by *Prosimulium* (spring), *Simulium*, *Epeorus* (Iron), *Baetis*, *Ephemerella*, *Rhyacophila* and net spinning Trichoptera (*Diplectrona*, *Polycentropus*). Tanytarsini chironomids were only common in riffle sites. Orthoclaadiinae chironomids were common at all sites, reflecting the diversity of this group, yet they were rarely most important. In impounded sites Chironomini and Tanytarsini chironomids were dominant replacing the Tanytarsini. Two non-Insecta taxa, *Psamanoryctides*

**Table 2.** Multiple regression models of CPOM, FPOM and VPOM on total density ( $NUMB$ ) and total biomass ( $BIO$ ) of invertebrates in each season. A stepwise procedure was used to select the best model (SAS Proc Stepwise, version 82.3). Only variables with significant  $F_{max}$  values were transformed. Regression equations for the autumn are not significant at 5%

Season	Model		R <sup>2</sup>
Spring	NUMB	= -76.73 + 0.40 (FPOM) + 107.23 (ln(VPOM))	72.4
	ln(BIO)	= 1.32 + 0.01 (FPOM) + 0.36 (ln(VPOM))	65.2
Summer	ln(NUMB)	= 4.14 + 0.58 (ln(VPOM))	79.8
	ln(BIO)	= -0.30 + 0.93 (ln(VPOM))	75.6
Autumn	NUMB	= 146.49 + 0.35 (ln(CPOM)) + 2.28 (FPOM)	31.6
	ln(BIO)	= -925.20 + 278.97 (ln(CPOM))	24.8



**Fig. 6.** Results of the cluster analysis showing the dendrogram for each season. Species assemblages are numbered from 1 to 12 in each season reflecting the linear arrangement of sample locations from the furthest downstream site (#1, a riffle) to the furthest upstream site (#12, a riffle). Site designations are as in Fig. 2

*californicum* (Oligochaeta) and *Pisidium* (Pelecypoda) were abundant in addition to predacious odonates (*Cordulegaster*) in impounded sites. These latter taxa are distributed in lentic, soft bottom habitats (Pennak 1978) and may exemplify a major change in community structure following habitat alteration by beaver.

Sprules (1940) reported that emergent insect assemblages differed following habitat alteration by beaver in a northern trout stream. A pronounced change in species from lotic to lentic types occurred. Hodkinson (1975a) also identified distinct faunal groups in habitats with varying degrees of beaver influence, and found species richness ( $S$ ; excluding chironomids) increased in sites with increased beaver influence. The opposite trend in diversity ( $H'$  and  $S$ ) is reported here. However, as cautioned by Naiman et al. (1984), samplers for emergent insects may tend to concen-

**Table 3.** Description of important taxa contributing to the benthic community of each site in each season. To be included a particular taxon required an IV of at least 10% in a site-season sample. Sum of IV may add to >100% since inclusion and data are from 3 independent samples (replicates) for each site-season combination. Only best IV for each taxon are reported

Spring	IV	Summer	IV	Autumn	IV
<b>Upstream riffle</b>					
<i>Prosimulium</i>	37.0	<i>P. californicum</i>	36.3	Tanytarsini	25.4
<i>Palpomyia</i>	27.5	Tanytarsini	27.4	<i>Epeorus (Iron)</i>	21.3
Orthocladiinae	25.3	Limnephilidae	25.4	<i>Rhyacophila</i>	19.2
<i>P. californicum</i>	18.1	Orthocladiinae	23.8	Orthocladiinae	17.6
<i>Epeorus (Iron)</i>	15.5	<i>Diplectrona</i>	21.4	<i>Simulium</i>	14.6
Tanypodinae	11.2			<i>Polycentropus</i>	12.4
				<i>Stenocron</i>	12.4
<b>Reach</b>					
<i>P. californicum</i>	62.1	<i>P. californicum</i>	52.2	<i>Cordulegaster</i>	44.7
<i>Cordulegaster</i>	25.5	<i>Cordulegaster</i>	33.7	Chironomini	42.9
Orthocladiinae	19.6	<i>Tipula</i>	30.1	<i>Tipula</i>	29.3
Chironomini	15.8	Chironomini	28.0	Orthocladiinae	15.3
<i>Pisidium</i>	12.3	Orthocladiinae	15.9	<i>P. californicum</i>	13.3
				<i>Parapsyche</i>	12.2
<b>Pond</b>					
<i>P. californicum</i>	50.0	<i>Cordulegaster</i>	36.4	<i>P. californicum</i>	62.3
Tanypodinae	18.7	<i>P. californicum</i>	35.9	Tanypodinae	25.0
Orthocladiinae	16.7	Tanypodinae	29.7	Chironomini	25.0
<i>Eurylophella</i>	14.3	Orthocladiinae	18.0	<i>Pisidium</i>	17.3
		Chironomini	10.6	<i>Cordulegaster</i>	15.7
				Cyclopoida	13.1
				<i>Sialis</i>	11.8
				<i>Palpomyia</i>	10.3
<b>Downstream riffle</b>					
<i>Epeorus (Iron)</i>	53.2	Orthocladiinae	47.6	<i>Tipula</i>	49.3
Tanytarsini	31.8	<i>Rhyacophila</i>	24.6	Tanytarsini	27.8
Orthocladiinae	18.5	Entomobryinae	10.6	Orthocladiinae	19.8
<i>Prosimulium</i>	14.2			<i>Eurylophella</i>	18.2
<i>Ephemerella</i>	14.1			<i>P. californicum</i>	17.3
<i>Simulium</i>	10.5			<i>Baetis</i>	14.6
				Enchytraeidae	10.3

trate individuals from many habitats, overestimating diversity in slow moving waters.

**Trophic relationships.** Collectors had a greater ( $P < 0.05$ ) biomass in impounded sites in all seasons and a higher density ( $P < 0.05$ ) in these sites in summer (Table 4). In no season were the IV's of collectors significantly different among sites. The large biomass of collectors in impounded sites was largely due to *P. californicum* (spring:  $\bar{x} = 51.83\%$ ; summer:  $\bar{x} = 36.5\%$ ; autumn:  $\bar{x} = 31.8\%$ ). Density, biomass and IV of collectors were tested for correlations with standing stocks of FPOM and VPOM. Significant ( $P < 0.01$ ) positive correlations (Spearman-Rank) were observed between collector density and biomass in all seasons with FPOM (min.  $r = 0.73$ ) and VPOM (min.  $r = 0.75$ ; not sig. for density in autumn). Collector IV was significantly ( $P < 0.01$ ) correlated with FPOM ( $r = 0.75$ ) and VPOM ( $r = 0.94$ ) in spring only.

Filters showed no significant differences between sites for any response variable in any season. The presence of filtering *Pisidium* in impounded sites and filter feeding *Simulium*, *Prosimulium* and net spinning caddisflies in riffle areas account for this result.

The principal predators in the pond were Tanypodinae, *Cordulegaster* and *Sialis*; in the reach *Cordulegaster*, *Dicranota*, *Hexatoma* and *Palpomyia* were common, while *Rhyacophila* was the most common predator in riffle sites. In spring and summer the density and biomass of predators were greater ( $P < 0.05$ ) in impounded sites (Table 4). In autumn no significant differences were observed in density and biomass among sites. In no season was the IV of predators different between sites. The correlation of predator density on potential prey density (i.e. density of all other sampled invertebrates) was significant ( $P < 0.04$ ) in all seasons (spring:  $r = 0.67$ ; summer:  $r = 0.80$ ; autumn:  $r = 0.75$ ). Predator biomass was significantly ( $P < 0.04$ ) correlated with potential prey density in spring ( $r = 0.65$ ) and summer ( $r = 0.58$ ). Predator IV was not significantly correlated with potential prey in any season.

Scrapers (eg. *Baetis*, *Epeorus (Iron)*) exhibited greatest densities ( $P < 0.05$ ) in riffle sites in all seasons. In summer and autumn IV's were greater in riffles than impounded sites. Scrapers were not abundant or important in impounded sites. Correlations of scraper density, biomass and importance on chlorophyll standing stock were not significant in any season.

**Table 4.** Distribution of invertebrates among functional feeding groups during each season. Tests of significance were between sites within feeding groups. Significance levels are given when  $P < 0.05$ . Density and biomass data were transformed as  $\ln(x + 1)$  and IV as  $2 * (\arcsine(x) / \pi)$  when necessary (Draper and Smith 1981). Densities and biomass are given as No. or  $\text{mg}/\text{m}^2$ . IV are %

Response variable	Feeding group	Upstream riffle	Reach	Pond	Downstream riffle	<i>P</i>
<b>Spring</b>						
Density	Collectors	744.3	9,284.0	7,736.7	2,769.7	n.s.
	Filterers	88.4	1,783.2	780.9	740.5	n.s.
	Predators	788.5	2,099.9	4,082.8	232.1	<0.01
	Scrapers	198.9	0.0	44.2	434.8	<0.01
	Shredders	33.1	110.5	419.9	99.5	n.s.
	Others	722.2	4,855.8	4,288.3	1,215.8	0.01
Biomass	Collectors	49.0	3,912.6	1,601.1	54.6	0.02
	Filterers	52.3	214.2	109.9	104.5	n.s.
	Predators	19.9	460.7	205.1	51.6	0.03
	Scrapers	48.5	0.0	13.7	110.5	n.s.
	Shredders	1.3	198.5	247.2	8.5	n.s.
	Others	6.6	194.4	174.3	24.9	<0.01
Importance value	Collectors	30.6	55.2	59.0	25.7	n.s.
	Filterers	29.7	8.3	4.2	18.7	n.s.
	Predators	22.5	15.3	17.1	7.9	n.s.
	Scrapers	19.5	0.0	0.4	32.8	n.s.
	Shredders	1.0	5.7	5.5	4.6	n.s.
	Others	20.0	19.3	16.0	20.3	n.s.
<b>Summer</b>						
Density	Collectors	1,562.2	23,342.7	14,898.6	2,018.8	<0.01
	Filterers	132.6	515.7	515.7	611.3	n.s.
	Predators	272.5	2,357.9	23,990.3	405.2	<0.01
	Scrapers	99.5	0.0	88.4	397.9	<0.01
	Shredders	309.5	309.5	221.1	258.0	n.s.
	Others	2,048.5	9,564.1	15,974.5	5,201.9	<0.01
Biomass	Collectors	54.7	2,237.1	1,566.6	50.5	<0.01
	Filterers	29.4	47.9	98.3	10.2	n.s.
	Predators	7.7	1,088.1	2,302.7	65.8	0.01
	Scrapers	2.9	0.0	23.0	25.8	n.s.
	Shredders	4.9	9.8	134.7	8.2	n.s.
	Others	28.7	1,149.7	130.6	73.8	n.s.
Importance value	Collectors	39.5	58.0	33.9	23.5	n.s.
	Filterers	15.6	1.2	1.6	4.7	n.s.
	Predators	6.9	15.7	46.9	12.0	n.s.
	Scrapers	2.6	0.0	0.3	8.6	<0.01
	Shredders	5.7	0.5	1.6	3.8	0.01
	Others	35.8	24.7	15.9	47.4	n.s.
<b>Autumn</b>						
Density	Collectors	4,266.2	13,749.2	5,769.4	3,455.6	n.s.
	Filterers	1,407.4	426.6	921.0	228.3	n.s.
	Predators	1,812.6	6,779.5	4,206.5	1,620.3	n.s.
	Scrapers	663.1	265.3	0.0	574.7	0.04
	Shredders	169.5	243.2	33.2	184.1	n.s.
	Others	4,818.9	8,164.0	2,144.2	1,856.8	n.s.
Biomass	Collectors	123.1	496.8	1,037.4	128.8	0.03
	Filterers	20.1	102.3	131.0	9.4	n.s.
	Predators	93.2	4,166.5	403.0	24.8	n.s.
	Scrapers	117.5	131.8	0.0	32.3	n.s.
	Shredders	22.7	5.1	1.8	3.4	n.s.
	Others	63.3	1,047.4	45.3	641.6	n.s.
Importance value	Collectors	32.8	38.0	54.0	37.9	n.s.
	Filterers	5.4	6.1	6.9	5.8	n.s.
	Predators	16.4	28.7	28.1	7.9	n.s.
	Scrapers	18.2	2.1	0.0	11.6	<0.01
	Shredders	3.5	0.5	0.2	2.0	<0.01
	Others	23.8	26.2	10.9	34.8	n.s.

Shredder density and biomass was not significantly different between sites in any season. However, in summer and autumn the IV of shredders was significantly greater (>100%) in riffle sites (eg. *Leuctra*) than impounded sites (eg. *Pycnopsyche*, *Lepidostoma*). Correlations of shredder density, biomass and importance on CPOM standing stock were not significant despite significant differences in CPOM between sites.

Hodkinson (1975a) suggested 3 trophic groups predominated in impounded sites; shredders, collectors and predators. The latter two groups were abundant in beaver altered sites in this study. The absence of shredders and the abundance of CPOM in impounded sites is surprising. Possibly the trophic group categorization of certain taxa (eg. *P. californicum*) is oversimplified. The gut contents of 10 *P. californicum* were examined. In every case detritus found in the gut was less than 1 mm in diameter. Naturally these food resources may have been >1 mm before ingestion. The exact placement of this taxon and perhaps others (eg. Enchytraeidae) require further investigation.

### Synthesis

The river continuum concept (RCC) (Vannote et al. 1980) was originally presented as a set of hypotheses to describe changes in the structure and function of lotic communities in a "pristine" (Statzner and Higler 1985) watershed along a stream order gradient. However, few pristine watersheds remain and little is known of their aboriginal characteristics. Historically, beaver were undoubtedly an important component of watersheds in North America (Naiman et al. 1985) being naturally distributed in virtually all fresh water habitats except the arctic tundra, peninsular Florida and the southwestern deserts (Jenkins and Busher 1979). Seton (1929) estimated that at least 60 million individuals inhabited North America before European settlement, averaging 4 beaver per km<sup>2</sup>.

Dam construction and wood input by beaver in low order streams generates many modifications to lotic habitats (Neff 1957; Naiman et al. 1985). In particular, dam construction increases the storage of organic (Fig. 4) and fine inorganic materials in impoundments (Francis et al. 1985). Correlated with the former is an increase in the density and biomass of the invertebrate community which reflects changes in community structure from lotic to lentic taxa. Many experimental studies have shown how variation in detrital standing stock and sediment particle size influence invertebrate community structure in streams (Egglshaw 1964; Rabeni and Minshall 1977; Minshall and Minshall 1977; Reice 1980; Culp et al. 1983; Culp and Davies 1985). Structurally invertebrate communities in beaver altered habitats are uncharacteristic of typical low order assemblages.

The invertebrate community represented in beaver modified sites differs functionally from RCC predictions (Vannote et al. 1980) for low order streams. Collectors and predators are most abundant in impounded sites reflecting increases in FPOM, VPOM and potential prey types. Shredders decrease in relative importance in impounded sites, perhaps due to inadequate velocity and substrate requirements, although CPOM is abundant. Filterers remain important in impounded sites, though taxa change, while scrapers are not represented. Together these results suggest that impounded sites are functionally similar to large order systems.

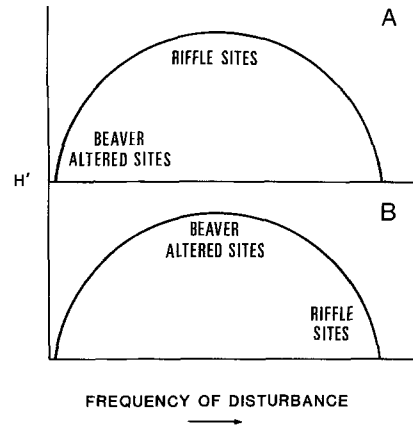


Fig. 7A, B. Theoretical relationship between species diversity and frequency of disturbance (Connell 1978; Ward and Stanford 1983). In both situations riffle sites are assumed to be more disturbed than beaver altered sites. **A** Riffle sites exhibiting maximum diversity and intermediate disturbance levels. **B** Beaver altered sites exhibiting maximum diversity, and intermediate disturbance levels

In a reformalization of the RCC, Minshall et al. (1985b) state that the model should be considered as a general theoretical construct in which to compare stream systems. "Regional and local deviations... are a predictable result of specific variation in climate and geology, tributary influences and local specific lithology and geomorphology, as well as changes imposed by man." Beaver modify stream geomorphology resulting in the deviation of many lotic properties associated with low order streams (Naiman et al. 1985). These effects alter invertebrate community structure and function resulting in a low order stream system more complex than is suggested by the RCC.

The construction of a dam in a previously unaltered stream imparts a disturbance to the system initially (Naiman et al. 1985). After dam construction, the impoundment progresses through a period of relatively little habitat alteration, the length of which is directly proportional to the residency of beaver. When the site is abandoned, the dam and pond begin to deteriorate (e.g. this study). Construction of a beaver impoundment may act to attenuate the influence of disturbance (drought or floods) on benthic community structure. This effect should be most pronounced during and immediately following (<1 yr) residency by beaver.

Ward and Stanford (1983) have applied the intermediate disturbance hypothesis (IDH) (Connell 1978) to lotic systems, as have others (Minshall et al. 1985a; Reice 1985), in an attempt to explain high species diversity. It can be hypothesized that impounded sites should exhibit reduced species diversity from competitive exclusions at low disturbance levels (Fig. 7a). On 1 of 3 occasions species diversity ( $H'$ ) was depressed in beaver altered sites (Fig. 5c). This hypothesis assumes 1) a competitive hierarchy (Connell 1978; Reice 1985) which leads to reduced diversities at low disturbance levels, and 2) that nonaltered sites are more disturbed than impounded sites, and in such a manner that greater diversities result in the former (Fig. 7a). However, the disturbance regime may be such that greatest diversities occur in beaver altered sites (Fig. 7b). The impounded sites in this study undergo tremendous fluctuations in water level as seasons change (Fig. 2) unlike a beaver occupied site. The testing of these assumptions will indicate whether the



IDH is an appropriate explanation for the observed diversity trends.

One important question remains. How dissimilar are beaver altered sites from naturally occurring pools in lotic systems? Certainly changes in channel geomorphology by dam construction, and canopy cover by flooding and harvest make this habitat potentially very unique. Naiman et al. (1984) suggested several characteristics of beaver ponds which may be unique, including longitudinal mixing patterns and nutrient enrichment from adjacent terrestrial systems. Preliminary results from an investigation of streams in the same watershed as Beaver Creek (Reice and Naiman 1986) suggest that the dominant taxa in alcove sites (rarely disturbed) in larger order streams (sixth) are similar to taxa (eg. *Pisidium*, *P. californicum*) reported here. These sites also have a preponderance of collectors and predators and few shredders. Invertebrate communities in beaver impoundments may not be unique within the watershed but likely represent unparalleled assemblages in low order streams.

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