

## Modification of stream ecosystem structure and function by beaver (*Castor canadensis*) in the Adirondack Mountains, New York

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Stream ecosystem structure and function were studied in an acidic second-order Adirondack Mountain stream system with current beaver activity. Acid-neutralizing capacity, pH, dissolved organic carbon,  $\text{Fe}^{2+}$ , and  $\text{Mn}^{2+}$  values were elevated and  $\text{SO}_4^{2-}$ ,  $\text{Al}^{3+}$ , and dissolved oxygen concentrations were decreased following water transport through the beaver impoundment. Upstream acidity was primarily ameliorated by  $\text{SO}_4^{2-}$  and Fe retention in the impoundment during the low-flow summer period. High Fe and Al sediment concentrations were present during low-flow periods immediately downstream of the beaver dam. During the high-flow period, Fe and Al concentrations were highest 0.25 km downstream of the dam, owing to slow metal hydrolysis–oxidation kinetics during spring snowmelt. The immediate downstream site exhibited significantly lower invertebrate richness and diversity and collector–filterer, Plecoptera, and Trichoptera densities, but significantly higher total invertebrate, Diptera, Ephemeroptera, predator, and collector–gatherer densities. Significant differences were noted primarily during April and July. Our results indicate that beaver dams modify stream ecosystems longitudinally and temporally and ameliorate stream acidity. Current lotic ecosystem paradigms like the river continuum concept should incorporate “patch” occurrences such as those created by beaver.

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La structure et le fonctionnement d'un écosystème d'eau courante ont été étudiés dans un ruisseau acide de second ordre modifié par la présence de castors dans les Adirondacks. La capacité de neutraliser l'acidité, le pH, et les concentrations de carbone organique dissous, de  $\text{Fe}^{2+}$  et de  $\text{Mn}^{2+}$  ont augmenté après le passage de l'eau dans le barrage de castor, alors que les concentrations de  $\text{SO}_4^{2-}$ , d' $\text{Al}^{3+}$  et d'oxygène dissous ont diminué. La baisse de l'acidité était attribuable surtout à la rétention du  $\text{SO}_4^{2-}$  et du Fe dans le barrage au cours de la période de l'étiage d'été. Les sédiments contenaient des concentrations élevées de Fe et d'Al immédiatement en aval du barrage au cours des périodes d'étiage. Durant la crue, c'est à 0,25 km en aval du barrage que les concentrations de Fe et d'Al étaient le plus élevées, en raison de la lenteur de l'hydrolyse–oxydation des métaux durant la fonte des neiges. À la station immédiatement en aval, on enregistrait une richesse et une diversité d'invertébrés significativement moindres et les densités de collecteurs filtreurs, de Plécoptères et de Trichoptères étaient plus faibles aussi, alors que le nombre total d'invertébrés et la densité des Diptères, Éphéméroptères, prédateurs et collecteurs rassembleurs était plus forte. Les différences significatives ont été enregistrées surtout en avril et en juillet. Nos résultats indiquent que les barrages de castors modifient les écosystèmes d'eau courante longitudinalement et temporellement et améliorent l'acidité des eaux. Les théories courantes sur les écosystèmes lotiques, telles le concept du continuum (river continuum concept), devraient tenir compte d'événements circonscrits comme ceux créés par la présence d'un barrage de castor.

[Traduit par la revue]

### Introduction

Beaver alter stream ecosystems in a variety of ways. Dam building results in retention of sediment and organic matter in the stream, creation of wetland areas with alteration of riparian habitat, modification of water and sediment chemistry dynamics, and modification of biotic community structure and function (Naiman and Melillo 1984; Naiman *et al.* 1984; McDowell and Naiman 1986; Naiman *et al.* 1986; Ford and Naiman 1988; Naiman *et al.* 1988a). Furthermore, beaver-induced alteration of stream ecosystem structure and function has brought into question the validity of a current lotic ecosystem paradigm, the river continuum concept (Vannote *et al.* 1980), and its later modifications (Minshall *et al.* 1985; Statzner and Higler 1985); briefly, this concept hypothesizes that lotic ecosystems are a linked continuum of physical gradients with which biotic components interact from upstream to downstream areas. This continuum is interrupted by dam building by beavers and its associated effects (Naiman *et al.* 1988b; Pringle *et al.* 1988).

Finally, beaver may facilitate amelioration of stream acidity

(Driscoll *et al.* 1987). Little attention has been focused on this aspect of beaver activity, but in areas of potential anthropogenic stream acidification (e.g., the northeastern United States and Canada), beaver may play a vital role.

The objectives of our research were to compare benthic invertebrate community structure and function, water chemistry, and sediment chemistry in a low-order acidic Adirondack Mountain stream system where there was current beaver activity. In addition, we discuss the role of beaver-induced modification in relation to mitigation of stream acidity and the river continuum concept.

### Study site and methods

Our study site was Pancake-Hall Creek and its tributaries, located in the western Adirondack Mountains, New York, U.S.A. (43°50'N, 74°52'W). The watershed area for Pancake-Hall Creek is 74 ha. The watershed contains primarily second-growth deciduous stands (*Acer saccharum*, *Fagus grandifolia*, *Betula alleghaniensis*) with small interspersed coniferous stands (*Picea rubens*, *Abies balsamea*, *Tsuga canadensis*). Surficial geology of the Pancake-Hall Creek watershed is generally characterized by acidic soil with shallow deposits (<3 m) of glacial till. However, deposits of thick (>3 m) till are evident near the lower portion of the catchment.

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TABLE 1. Yearly values for water physical-chemical parameters from January 1985 to January 1986 (except for Fe, Mn, and Zn values, which are from January 1985 to October 1985)

	PAT	PA2	PA3
Temperature (°C)	5.7 (0.0–14.0)	6.8 (0.0–18.0)	6.7 (0.0–16.0)
Velocity (m·s <sup>-1</sup> )	0.21 (0.13–0.30)	0.27 (0.15–0.32)	0.39 (0.28–0.52)
Dissolved O <sub>2</sub> (% saturation)	92 (88–96)	77 (68–86)	91 (85–97)
Benthic organic matter (>250 µm) (mg/sample)	1786 (809–4285)	2382 (1274–3556)	1403 (445–2729)
pH	4.88 (4.53–5.80)	5.26 (4.68–5.94)	5.41 (4.72–6.38)
Acid-neutralizing capacity (µequiv·L <sup>-1</sup> )	–5.9 (–18.3 to 21.5)	25.2 (–12.1 to 120.1)	18.4 (–10.9 to 72.4)
Total monomeric Al (mg·L <sup>-1</sup> )	0.52 (0.09–0.91)	0.27 (0.08–0.46)	0.27 (0.08–0.49)
Inorganic monomeric Al (mg·L <sup>-1</sup> )	0.38 (0.04–0.63)	0.15 (0.03–0.25)	0.14 (0.03–0.30)
Organic monomeric Al (mg·L <sup>-1</sup> )	0.14 (0.05–0.28)	0.12 (0.06–0.21)	0.12 (0.05–0.19)
Fe (mg·L <sup>-1</sup> )	0.14 (0.03–0.71)	0.85 (0.23–1.66)	0.38 (0–1.03)
Mn (mg·L <sup>-1</sup> )	0.08 (0.06–0.19)	0.12 (0.06–0.40)	0.10 (0–0.34)
Zn (mg·L <sup>-1</sup> )	0.05 (0–0.09)	0.06 (0.01–0.31)	0.03 (0–0.09)
Basic cations (µequiv·L <sup>-1</sup> )	149.1 (99.0–201.9)	154.0 (94.7–199.8)	164.1 (109.0–212.1)
SO <sub>4</sub> <sup>2-</sup> (mg·L <sup>-1</sup> )	7.33 (6.74–8.73)	5.62 (2.09–7.95)	5.90 (2.54–7.84)
NO <sub>3</sub> <sup>-</sup> (mg·L <sup>-1</sup> )	0.50 (0.09–1.30)	0.28 (0.02–0.92)	0.40 (0.09–1.19)
Dissolved organic carbon (mg C·L <sup>-1</sup> )	3.61 (2.38–4.65)	6.60 (3.68–12.32)	5.90 (3.28–12.07)

NOTE: Values are given as the mean, followed by the range in parentheses.

Three second-order sampling sites were selected. PAT was located at the confluence of two first-order tributaries to Pancake-Hall Creek, the second-order tributary emptying into an impoundment with current beaver activity, PA2 was situated immediately downstream (1 m) of the beaver dam, and PA3 was approximately 0.25 km downstream of PA2. The substrate at each site was similar, consisting primarily of cobbles overlying gravel and sand.

Benthic invertebrates were collected quarterly from January to October 1985, using a modified Hess sampler (0.1 m<sup>2</sup>; 250-µm mesh) in shallow, center riffle areas of comparable depth and width. Five replicates were collected at each site and immediately preserved in 95% ethanol for later sorting in the laboratory. Organisms were assigned to appropriate functional feeding groups according to Merritt and Cummins (1984) or by means of analysis of gut contents (Cummins 1973). Benthic organic matter (BOM; >250 µm) was measured from Hess samples by loss on combustion (450°C for 24 h) after invertebrates were removed.

Water samples were collected monthly and concurrently with biological samples during quarterly periods. Procedures for water collection and chemical analysis can be found in Driscoll *et al.* (1987).

Fine-grained sediments were collected during early June and September 1985. Collections were size-fractionated in the laboratory;

sediment in the 56- to 250-µm size range was analyzed. Organically bound Al and Fe, hydrous oxides of Al and Fe, and exchangeable Al were measured by direct-coupled plasma optical emission spectrophotometry after extraction using sodium pyrophosphate, ammonium oxalate, and potassium chloride, respectively (Cappo *et al.* 1987). Al- and Fe-bound organic carbon was determined by organic carbon analysis of sodium pyrophosphate extracts.

Analysis of variance (ANOVA) was used to determine significant differences in water chemistry and invertebrate parameters among sites. Duncan's multiple range test was used to detect differences among treatments when the overall ANOVA was significant ( $p < 0.05$ ). Invertebrate density data were transformed prior to statistical analysis using a logarithmic ( $x + 1$ ) transformation (Elliott 1977). Generic diversity was calculated using the Shannon–Wiener index (Weber 1973). Generic richness and diversity were underestimated because Chironomidae were excluded from the calculations, but provide for comparisons between sampling sites.

## Results

### Water chemistry

PAT was an acidic site (acid-neutralizing capacity (ANC)  $\leq 0$  µequiv·L<sup>-1</sup>) with concomitant low pH, basic cations (C<sub>B</sub>;

TABLE 2. Comparison of water physical-chemical parameters between sites PAT, PA2, and PA3 for summer (July-September), nonsummer (October-June), and annual periods, using ANOVA and Duncan's multiple range test

Parameter	Annual	Summer	Nonsummer
Temperature	ns	* PA2, PA3 > PAT	ns
Velocity	ns	ns	ns
Benthic organic matter	ns	ns	ns
Dissolved O <sub>2</sub>	** PAT, PA3 > PA2	** PAT, PA3 > PA2	** PAT, PA3 > PA2
pH	** PA2, PA3 > PAT	** PA2, PA3 > PAT	* PA2, PA3 > PAT
Acid-neutralizing capacity	** PA2, PA3 > PAT	** PA2, PA3 > PAT	ns
Basic cations	* PA3 > PAT	ns	** PA3 > PAT
SO <sub>4</sub> <sup>2-</sup>	** PAT > PA2, PA3	** PAT > PA2, PA3	ns
NO <sub>3</sub> <sup>-</sup>	* PAT > PA2	ns	ns
Dissolved organic carbon	** PA2, PA3 > PAT	** PA2, PA3 > PAT	ns
Total monomeric Al	** PAT > PA2, PA3	ns	** PAT > PA2, PA3
Inorganic monomeric Al	** PAT > PA2, PA3	ns	** PAT > PA2, PA3
Organic monomeric Al	ns	ns	ns
Fe	** PA2 > PAT, PA3	—	—
Mn	ns	—	—
Zn	ns	—	—

NOTE: \*,  $p < 0.05$ ; \*\*,  $p < 0.01$ ; ns, not significant.

Ca<sup>2+</sup>, Mg<sup>2+</sup>, Na<sup>+</sup>, K<sup>+</sup>), and high total monomeric Al, inorganic monomeric Al, SO<sub>4</sub><sup>2-</sup>, and NO<sub>3</sub><sup>-</sup>. Both PA2 and PA3 were less acidic (ANC > 0 μequiv. · L<sup>-1</sup>), with similar water physical-chemical characteristics, although there was lower dissolved oxygen (DO) and higher concentrations of Fe at PA2 (Table 1). Dissolved oxygen was also measured in the beaver pond; the annual mean value was 50% (range 38–56%) saturation. Mean annual water physical-chemical parameters show significant ( $p < 0.01$ ) differences in DO and Fe between PA2 and both of the other sites, while both PA2 and PA3 had significantly ( $p < 0.01$ ) higher pH, ANC, and dissolved organic carbon (DOC) than PAT (Table 2). Conversely, PAT had significantly ( $p < 0.01$ ) higher SO<sub>4</sub><sup>2-</sup>, total monomeric Al, and inorganic monomeric Al than PA2 and PA3. Seasonal differences among sampling sites were evident for pH, ANC, C<sub>B</sub>, SO<sub>4</sub><sup>2-</sup>, DOC, total monomeric Al, and inorganic monomeric Al (Table 2).

#### Sediment chemistry

Sediment chemistry exhibited pronounced seasonal differences (Table 3). At all sites, concentrations, except of exchangeable Al, were higher in September than in June. June trends were PA3 > PAT > PA2. Conversely, September trends were PA2 > PA3 > PAT (Table 3).

#### Invertebrates

Total invertebrate density was significantly higher at PA2

TABLE 3. Sediment analyses at the three sites

	PA2	PA3	PAT
June			
Organically bound Al	59	136	112
Organically bound Fe	57	115	50
Hydrous oxides of Al	46	80	73
Hydrous oxides of Fe	39	101	67
Al- and Fe-bound organic C	811	1419	886
Exchangeable Al	2.7	1.9	2.3
September			
Organically bound Al	263	193	237
Organically bound Fe	1066	271	126
Hydrous oxides of Al	723	191	237
Hydrous oxides of Fe	786	381	217
Al- and Fe-bound organic C	3485	2091	1786
Exchangeable Al	2.2	1.8	1.8

NOTE: Values are given in micromoles per gram of dry weight, as the mean of triplicate analyses.

than at PA3 ( $p < 0.001$ ) and PAT ( $p < 0.05$ ) during July, but significantly ( $p < 0.05$ ) lower than at PA3 during April. Diptera density was significantly higher at PA2 than at PA3 during January ( $p < 0.01$ ), July ( $p < 0.001$ ), and October ( $p < 0.05$ ), and significantly ( $p < 0.01$ ) higher than at PAT during July.

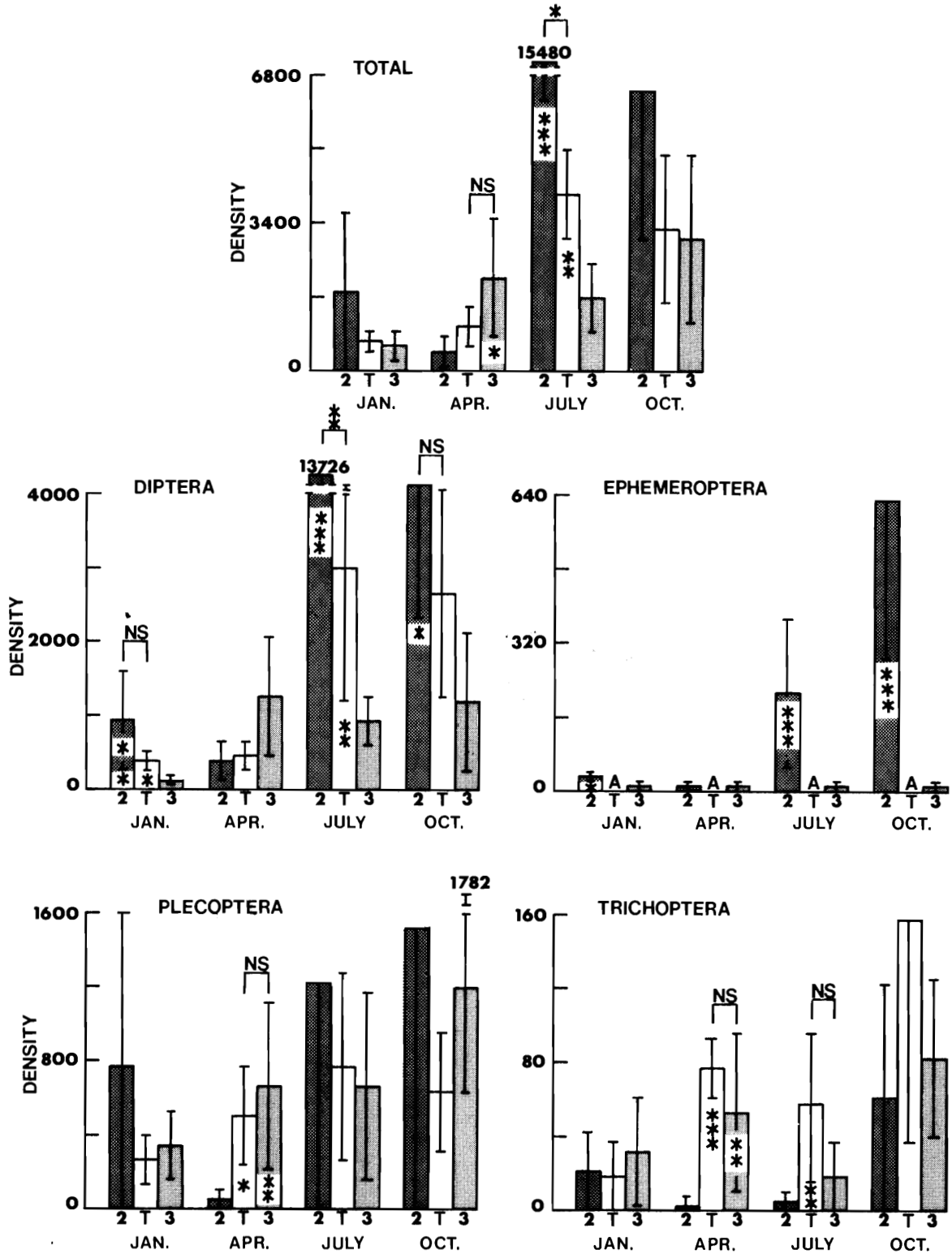


FIG. 1. Mean density of total benthic invertebrates and insect orders according to sampling date. Density is the number of individuals per sample. T, 2, and 3 indicate sites PAT, PA2, and PA3, respectively. A, absent. \*,  $p < 0.05$ ; \*\*,  $p < 0.01$ ; \*\*\*,  $p < 0.001$ ; NS, not significant (Duncan's multiple range test). Error bars are  $\pm 1$  SD.

Most of the Diptera collected at all sites were Chironomidae. During January, July, and October, Ephemeroptera density was significantly ( $p < 0.05$ ,  $p < 0.01$ ,  $p < 0.01$ , respectively) higher at PA2 than at the other two sites. Plecoptera density was significantly higher at PA3 ( $p < 0.001$ ) and PAT ( $p < 0.05$ ) than at PA2 during April. Finally, Trichoptera density was significantly higher at PAT ( $p < 0.001$ ) and PA3 ( $p < 0.01$ )

than at PA2 during April; density was significantly ( $p < 0.01$ ) higher at PAT than at PA2 during July (Fig. 1).

Collector-filterer density was significantly ( $p < 0.05$ ) higher at PAT and PA3 than at PA2 during April only. During January, July, and October, PA2 exhibited significantly ( $p < 0.01$ ,  $p < 0.001$ ,  $p < 0.01$ , respectively) higher predator density than PA3. In April, predator density was significantly ( $p < 0.05$ )

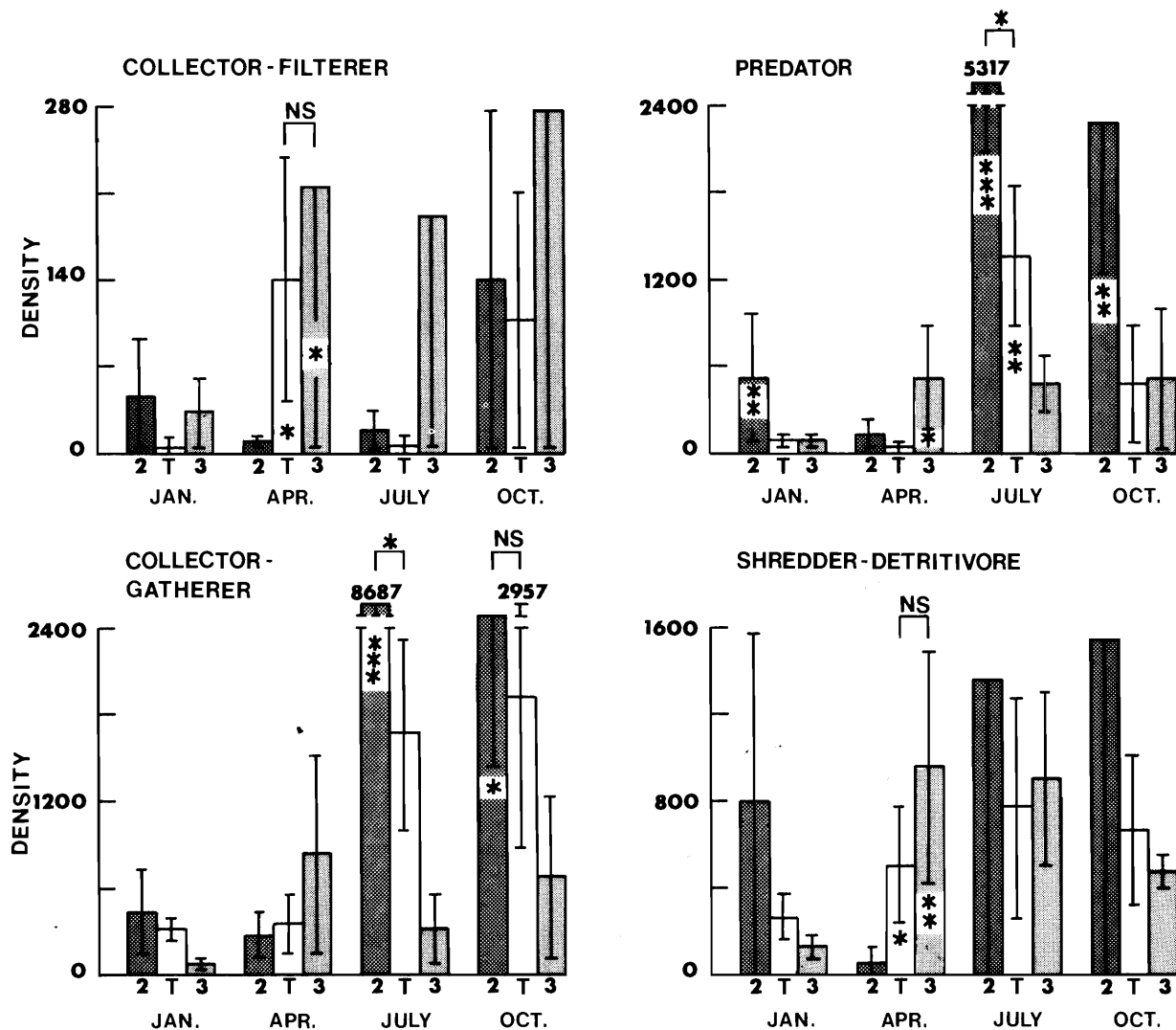


FIG. 2. Mean functional feeding group density according to sampling date. Density is the number of individuals per sample. \*,  $p < 0.05$ ; \*\*,  $p < 0.01$ ; \*\*\*,  $p < 0.001$ ; NS, not significant (Duncan's multiple range test). Error bars are  $\pm 1$  SD.

higher at PA3 than at either PA2 or PAT. Collector-gatherer density was significantly higher at PA2 during July ( $p < 0.001$ ) and October ( $p < 0.05$ ). Only during April were there significant differences in shredder-detritivore density; PA3 ( $p < 0.01$ ) and PAT ( $p < 0.05$ ) had significantly higher densities than PA2 (Fig. 2). Scrapers were never abundant and always composed  $< 1\%$  of total invertebrate density. Both PAT and PA3 showed significantly ( $p < 0.05$ ) higher generic richness during April and July (Fig. 3).

Diversity was decreased at PA2 during April and July. Comparable diversity values were calculated during January at all sites. PA3 exhibited increased diversity during October (Table 4).

### Discussion

Beaver modify stream ecosystem structure and function in a variety of ways in Pancake-Hall Creek. Generally, pH, ANC, DOC, Fe, and Mn values were elevated and DO,  $\text{SO}_4^{2-}$ , and Al concentrations were decreased following water transport through the beaver impoundment. DO was reduced in the beaver impoundment, presumably as a result of increased organic matter retention and associated decomposition processes (Naiman *et al.* 1986; Naiman *et al.* 1988a). Outflow from the

beaver dam resulted in immediate, albeit incomplete, oxygenation at PA2. Complete reoxygenation was accomplished by PA3; thus, prolonged longitudinal deprivation of oxygen was not evident and would not be expected in a clean, low-order woodland stream.

Increased ANC at PA3 can be partially attributed to thicker till soils in this area of the catchment, but the role of  $C_B$  in the increase of ANC was negligible at PA2 and is a result of microbial reduction processes occurring in the impoundment. Retention of  $\text{SO}_4^{2-}$  primarily, and enrichment of reducible metals ( $\text{Fe}^{2+}$ ,  $\text{Mn}^{2+}$ ) secondarily, at PA2, owing to the impoundment, were generally responsible for the mitigation of stream acidity (Driscoll *et al.* 1987). Measured increases in ANC were not as large as expected from the extent of  $\text{SO}_4^{2-}$  retention and  $\text{Fe}^{2+}$ - $\text{Mn}^{2+}$  release. Hydrolysis of Al and release of organic acids also occurred within the beaver impoundment and attenuated ANC increases. The release of reducible metals is not a permanent source of ANC, as they will eventually oxidize and hydrolyze in well-oxygenated stream water, resulting in reacidification (Stumm and Morgan 1981).

Differences in ANC among sites were only evident in the low-flow summer period. Retention of S within the beaver impoundment was likely due to microbial activity and was

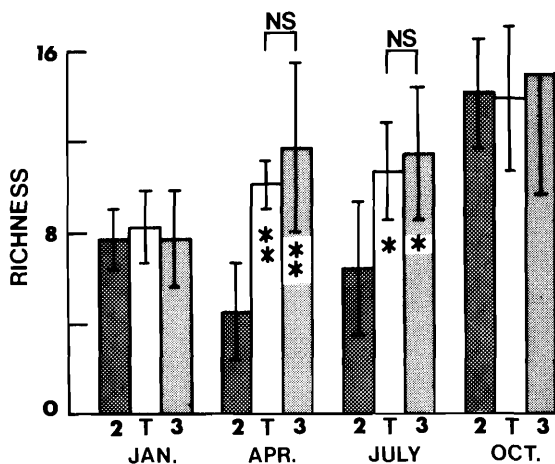


FIG. 3. Seasonal mean generic richness of benthic invertebrates, i.e., the number of genera per sample. \*,  $p < 0.05$ ; \*\*,  $p < 0.01$ ; NS, not significant (Duncan's multiple range test). Error bars are  $\pm 1$  SD.

TABLE 4. Shannon-Wiener diversity index values according to sampling date, calculated from pooled data (five replicates) at each site

	Jan.	Apr.	July	Oct.
PA2	2.10	1.16	1.45	2.13
PAT	2.13	2.45	1.81	2.07
PA3	2.00	2.22	2.35	2.88

enhanced by the relatively long hydraulic retention time and higher temperatures during this time period. During the summer period, reduced flow exposes some organic deposits but oxidation of reduced S was not extensive because there were no pulsed increases of  $\text{SO}_4^{2-}$  during increased autumn discharge periods (Driscoll *et al.* 1987). Thus, the beaver impoundment served as a sink for  $\text{SO}_4^{2-}$  during the low-flow summer period and was not a major source of  $\text{SO}_4^{2-}$  at any time during the annual cycle.

In our study, sediment chemistry was also influenced by beaver. Generally, organically bound Fe concentrations were elevated at sites below the beaver impoundment, owing to elevated concentrations of exported Fe and organic matter. Early-June sediment samples reflected high-flow nonsummer water conditions. Sediment metal and carbon concentrations were low and are consistent with the water chemistry conditions discussed previously. Lower ANC during this period results in relatively slow oxidation kinetics of metals in acidic solutions, especially those containing complexing ligands; thus, deposition to stream sediments may occur over a relatively long stream reach, resulting in highest concentrations at PA3 (Stumm and Morgan 1981). In addition, increased stream discharge results in easier transport of precipitates and material to downstream reaches (Hynes 1970). Material exported from the impoundment may not have time to physically settle out at PA2. Upon visual observation of substrate at PA2 during this seasonal period, no obvious Fe precipitates were present.

September sediment samples reflected low-flow summer water chemistry conditions. PA2 sediment metal and carbon concentrations were highest in September and measured sediment parameters were much higher at all sites during this

sampling. Increased ANC and higher temperature resulted in faster oxidation kinetics of the metals and consequent deposition at PA2. The substrate at PA2 exhibited a thick covering of brick-red precipitates during this sampling period, presumably a result of Fe deposition.

Benthic invertebrate community structure and function were also altered as a result of stream modification by beaver. Generally, densities of total invertebrates, Diptera, Ephemeroptera, predators, and collector-gatherers were increased, and densities of Trichoptera, Plecoptera, and collector-filterers and generic richness and diversity were decreased at PA2. Amelioration of acidity by the beaver impoundment is an important factor in benthic invertebrate community differences between PA2 and PAT. Acidic streams are often characterized by an absence or reduction in density of Ephemeroptera and an increased density of Trichoptera (Haines 1981), as observed in this study.

PA2 and PA3 invertebrate communities were directly influenced by the beaver impoundment. High concentrations of Fe exported from the beaver impoundment resulted in increased downstream water and sediment Fe concentrations. High concentrations of trace metals and deposition of Fe to the substrate have been shown to decrease invertebrate richness and diversity (Hynes 1970). Low DO at PA2 may also deleteriously affect invertebrate community richness and diversity (Hynes 1970).

Benthic organic matter, although not significantly different among sites, owing to a large variance in our data, was more prevalent at PA2 from export of impoundment deposits. The presence of detrital standing stocks has been positively correlated with benthic invertebrate density (Egglshaw 1964; Culp and Davies 1985). Increased BOM at PA2 may be responsible for high densities of total invertebrates and certain taxa or feeding groups dependent on detritus, such as collector-gatherers, many chironomid Diptera, and Ephemeroptera.

Decreases in collector-filterer density at PA2 may appear anomalous considering the large export of organic matter from the impoundment, but are presumably due to metal precipitate deposition which can clog filtering apparatus and have direct toxic effects. By PA3, conditions were conducive to significantly higher collector-filterer densities.

Seasonal trends in invertebrate parameters were remarkably similar among the three sampling sites. July and October densities were generally highest at each site; most differences among sites were evident during April and July, owing to unique water and sediment characteristics at each site during low- and high-flow stream conditions.

Our results indicate that water physical-chemical parameters, sediment chemistry, and benthic invertebrate community structure and function are modified in Pancake-Hall Creek as a result of beaver activity. Other studies have shown that beaver can modify stream ecosystems in a variety of ways (Naiman *et al.* 1984; McDowell and Naiman 1986; Naiman *et al.* 1986; Naiman *et al.* 1988a; Ford and Naiman 1988), leading to questions concerning the efficacy of current lotic ecosystem paradigms such as the river continuum concept (Vannote *et al.* 1980) and resource spiralling (Elwood *et al.* 1983) as predictive tools. Current studies are attempting to incorporate the effects of beaver activity and other stream "patch" occurrences into these paradigms (Johnston and Naiman 1987; Naiman *et al.* 1988b; Pringle *et al.* 1988). Furthermore, longitudinal effects can extend appreciably beyond the immediate downstream areas of beaver dams, as evidenced in our study. Long-term temporal

effects of beaver activity are well documented (Ruedemann and Schoonmaker 1938; Naiman *et al.* 1988a); we also observed a distinct seasonal influence of beaver on stream abiotic and biotic parameters. Finally, beaver appear to play an important role in mitigating stream acidity and should therefore be incorporated into current research and modeling of stream acidification.

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