



Benthic macroinvertebrate response to sedimentation in a *Typha angustifolia* L. wetland

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Abstract

Fiberglass mesh enclosures ($1 \times 1 \text{ m}^2$) in a *Typha angustifolia* L. marsh were employed to examine the effects of clay additions on the resident macroinvertebrate communities. Total invertebrate density, insect density, and number of insect families decreased significantly by 33%, 37%, and 17%, respectively, in enclosures receiving sediment. More specifically, incoming clay adversely affected densities of Coleoptera larvae, Diptera larvae, Megaloptera larvae, Odonata larvae, Pelecypoda, and Gastropoda. Densities of specific families within the Diptera (larvae) and Coleoptera were also affected; Dolichopodidae, Stratiomyidae, Hydrophilidae, Tabanidae, Dytiscidae adults, and Scirtidae larvae decreased significantly in numbers in sedimented enclosures. In contrast, the effect of sedimentation on Carabidae (adults and larvae) and Dytiscidae larval densities varied significantly with time, whereby densities were higher in the sedimented treatment only for the initial two months of the study. Densities of predator-engulfer, collector-filterer, and scraper feeding groups were reduced in sedimented plots by 28%, 44%, and 27%, respectively. Significant short- and long-term increases in turbidity and suspended solids in enclosures treated with clay, as well as sediment deposition, were probably responsible for changes in the invertebrate communities.

Introduction

In lotic habitats, the influence of sedimentation on benthic macroinvertebrates has been subjected to detailed study. In these systems, declines in invertebrate density and taxonomic richness, accompanied by shifts in taxonomic composition, are generally associated with acute sedimentation (Nuttall and Bielby, 1973; Gray and Ward, 1982; Lenat, 1984; Quinn et al., 1992; and others). Such studies have demonstrated that the invertebrate fauna of rivers and streams is affected by sedimentation via various indirect and direct mechanisms. Direct mechanisms include loss of invertebrate habitat, burial of invertebrates, burial of major food sources, (e.g., detritus – Lenat et al., 1981), and accumulation of particles on respiratory and feeding structures of macroinvertebrates (Lemly, 1982). Indirect mechanisms include those changes that alter the productivity of algae, bacteria and fungi, as well as

those that affect the decomposition of plant detritus, (e.g., elevated regimes of suspended material, reductions in oxygen and pH and introduction of pollutants adsorbed to sediment particles – Boto and Patrick, 1978; Lenat et al., 1981; Lemly, 1982; Davies-Colley et al., 1992; Quinn et al., 1992). In the absence of significant flow regimes in lentic wetland systems, the potential for disruption of the benthic macroinvertebrate community seems even more applicable by both direct and indirect means.

Sediment retention within a wetland basin is considered an important and beneficial functional feature of wetlands (Bhowmik and Demissie, 1986; Kuenzler, 1989; Fennessy et al., 1994; Kleiss, 1996); however, natural and human-induced sedimentation events in wetlands (e.g., from urbanization and agricultural activity – Martin and Hartman, 1987; Ewing, 1996) also result in numerous ecological consequences (Johnston et al., 1984). With regard to wetland flora,

recent studies have documented sediment-induced alterations in seed germination (Neely and Wiler, 1993; Jurik et al., 1994; Wang et al., 1994; Dittmar and Neely, 1999), plant productivity (van der Valk et al., 1983; Ewing 1996), and plant decomposition (Vargo et al., 1998). In comparison, critical questions regarding the response of wetland fauna to sedimentation have remained essentially unaddressed. Given the importance of aquatic invertebrates to waterfowl management, control of invasive plant species, food chain support, and detrital processing, as well as their use as environmental indicators (Krull, 1970; Krapu, 1974; Euliss and Harris, 1987; Murkin and Kadlec, 1986; Murkin and Batt, 1987; Batzer and Wissinger, 1996), this seems a significant oversight. Furthermore, in comparison to lotic habitats, the absence, or at least substantial reduction, of flow may further accentuate the effects of sedimentation in wetlands. The objective of this study was to examine the influence of sedimentation on the benthic macroinvertebrate community in a natural *Typha* wetland. In this paper, we compare the invertebrate assemblages between unsedimented field enclosures and experimental enclosures exposed to sediment (clay) deposition. In addition, the effect of sediment addition on various water quality parameters is described.

Methods

This study was conducted in a cattail (*Typha angustifolia* L.) marsh adjacent to Independence Lake (42°24'30"N, 83°48'30"W, Washtenaw County, Michigan, USA) during the 1995 growing season (Martin, 1996). At the end of the growing season, *Typha* density was counted in ten unsedimented enclosure treatments (see enclosure description below). From outside the enclosures, fourteen *Typha* culms were collected to determine the average biomass/culm. Total *Typha* biomass (g m^{-2}) in enclosures was estimated from the product of average culm weight (g) and average culm density (m^{-2}).

Fifty square 1-m² fiberglass mesh enclosures were erected in a grid (ten rows of five plots) in early May, 1995. The fiberglass mesh protruded approximately 75 cm above the wetland floor and was anchored approximately 10 cm into the sediment by use of small wooden stakes to which the fiberglass was stapled. Twenty-five of these enclosures were randomly selected to receive sediment (clay) applications and the

Table 1. Benthic macroinvertebrates observed in experimental plots during the 1995 growing season within a *Typha angustifolia* L. wetland at Independence Lake, Michigan. Invertebrates were keyed to a taxonomic level sufficient for placement in a functional feeding group (see Table 5).

Ephemeroptera	Trichoptera
Baetidae ^a	Limnephilidae ^a
Odonata	Lepidoptera
Coenagrionidae ^{a,b}	Noctuidae ^{a,b}
Aeshnidae ^a	Tortricidae ^a
Libellulidae ^{a,b}	
Hemiptera	Diptera
Belostomatidae ^b	Ceratopogonidae ^{a,b}
Hebridae ^b	Chironomidae ^{a,b}
Pleidae ^a	Culicidae ^{a,b}
Veliidae ^{a,b}	Dolichopodidae ^a
	Empididae ^a
	Ephydriidae ^{a,b}
Megaloptera	Ptychopteridae ^a
Corydalidae ^{a,b}	Sciomyzidae ^{a,b}
	Stratiomyidae ^{a,b}
Coleoptera – larvae	Syrphidae ^{a,b}
Carabidae ^{a,b}	Tabanidae ^{a,b}
Dytiscidae ^{a,b}	Tanyderidae ^b
Halplidae ^a	Tipulidae ^{a,b}
Hydrophilidae ^{a,b}	
Lampyridae ^{a,b}	Collembola
Scirtidae ^{a,b}	Entomobryidae ^{a,b}
Staphylinidae ^{a,b}	
	Acarina – Hydrachnellae^{a,b}
Coleoptera – adults	Annelida – Hirudinea^{a,b}
Anthicidae ^{a,b}	Glossiphoniidae ^{a,b}
Carabidae ^{a,b}	Erpobdellidae ^{a,b}
Curculionidae ^{a,b}	
Dryopidae ^b	Annelida – Oligochaeta^{a,b}
Dytiscidae ^{a,b}	
Forficulidae ^a	Pelecypoda – Sphaeriidae^{a,b}
Histeridae ^b	
Halplidae ^{a,b}	Gastropoda^{a,b}
Hydraenidae ^{a,b}	
Hydrophilidae ^{a,b}	
Scirtidae ^{a,b}	
Staphylinidae ^{a,b}	

^a Occurred in unsedimented, control plots.

^b Occurred in sedimented treatment plots.

remaining enclosures were left undisturbed as control plots.

Clay (Goldart clay – mined in Ohio, and distributed by Rovin Ceramics – see Vargo et al., 1998) was applied biweekly from May–August. Clay was brought into the wetland in pre-measured packages (726 g each) on each application date and mixed with 1–2 liters of water from each enclosure receiving sedimentation. This slurry was gently and homogeneously applied throughout the enclosure from which the water had been taken.

From June until September, invertebrates were sampled at the end of each month from three randomly-chosen enclosures of each treatment (sedimented and unsedimented). Before each enclosure was sampled, all emergent vegetation protruding above the air-water interface was cut and discarded. The remaining vegetation, which included senesced cattails lying on the water surface and basal portions of living cattail stalks beneath the water, was cut at the sediment-water interface and placed in bags for sorting of invertebrates in the laboratory. After removal of the vegetation, collection of invertebrates continued with ten separate sweeps of the entire enclosure with a collection net; the sweeps included a thorough sampling of the substrate and associated detritus (approx. 2–3 cm into sediment). All samples were transported to the laboratory and stored at 5 °C. After having been sampled, an enclosure was no longer used in the study (i.e., destructive sampling of enclosures).

Within two weeks after collection, samples were hand-sorted by sugar floatation (52.27 kg of sugar per 20 liters of water – Anderson, 1959) and invertebrates were stored in 70% ethyl alcohol for later identification. Invertebrates were identified to the taxonomic level needed for assignment to a functional feeding group with the following dichotomous keys: Ward and Whipple (1959), Hilsenhoff (1981), Pennak (1989), and Merritt and Cummins (1996). Functional-feeding groups were determined from information in Merritt and Cummins (1996) and from our interpretation of life history descriptions in Pennak (1989).

On the days of sediment application, three randomly-selected enclosures for each treatment were selected for water quality sampling. Measurements and samples were taken from these six enclosures immediately before and within 24 hours after each sedimentation event. Temperature, dissolved oxygen, and pH were measured in the field with a YSI Model 57 temperature-oxygen meter and a Cole-Parmer Model 5941-00 pH meter. Additionally, two water samples

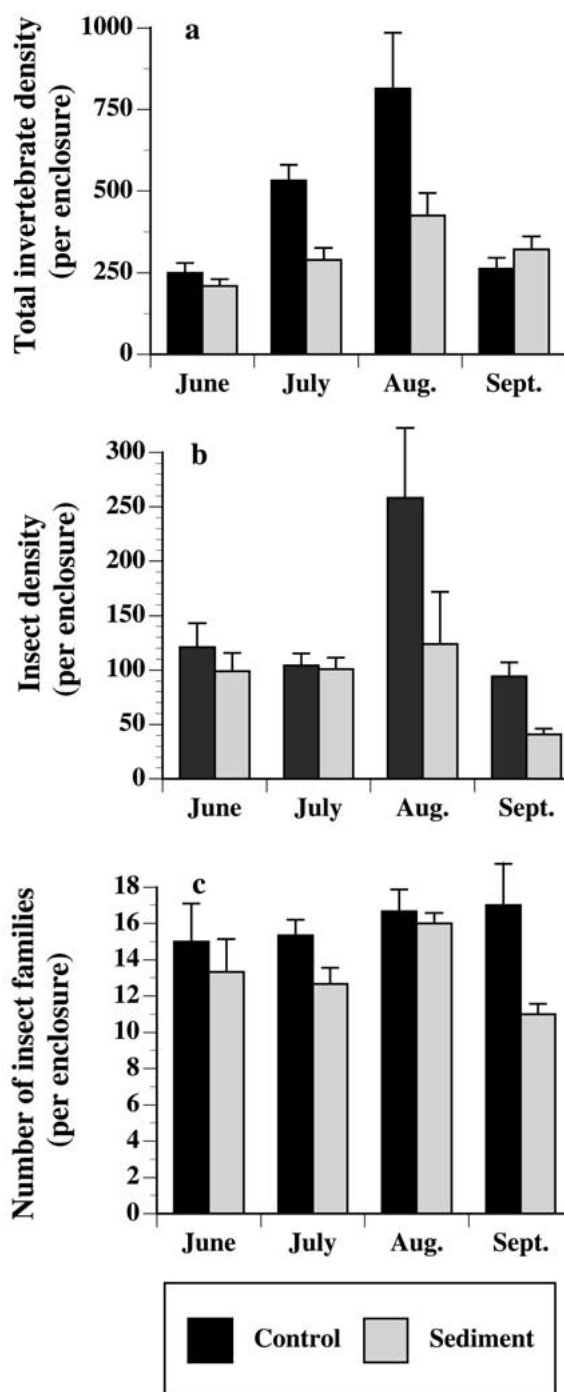


Figure 1. Average total invertebrate density (a), insect density (b), and number of insect families (c) collected from experimental enclosures within a *Typha angustifolia* L. wetland at Independence Lake during 1995 (\pm SE, $n = 3$).

Table 2. Degrees of freedom, F-value and statistical significance for ANOVAs of invertebrate densities collected from sedimented and unsedimented enclosures in a *Typha angustifolia* L. Marsh at Independence Lake in 1995.

	Total Invert. Density	Insect Density	# of Insect Families	Pelecypoda	Gastropoda	Diptera larvae	Megaloptera larvae	Coleoptera larvae	Odonata larvae
EFFECT	d.f. F	F	F	F	F	F	F	F	F
Date	3 11.38 ^a	5.76 ^b	1.27	9.27 ^a	46.44 ^a	9.34 ^a	0.85	39.71 ^a	0.71
Treatment	1 8.97 ^b	5.88 ^c	7.36 ^c	5.61 ^c	9.10 ^b	4.05 ^d	3.63 ^d	4.50 ^c	3.00 ^d
Date*Treatment	3 3.86 ^c	1.77	1.30	5.32 ^c	11.49 ^a	1.40	1.46	0.11	0.12
		Dolichopodidae	Stratiomyidae	Hydrophilidae	Tabanidae	Dytiscidae adults	Dytiscidae larvae	Carabidae	Scirtidae larvae
	d.f. F	F	F	F	F	F	F	F	
Date	3 1.14	0.30	27.72 ^a	4.49 ^c	3.75 ^c	29.92 ^a	5.74 ^a	18.87 ^a	
Treatment	1 5.39 ^c	5.32 ^c	3.43 ^d	3.52 ^d	8.45 ^b	0.78	0.24	4.55 ^c	
Date*Treatment	3 1.14	0.32	1.26	0.89	0.28	9.99 ^a	3.34 ^d	0.38	

^a = $p \leq 0.001$; ^b = $p \leq 0.01$; ^c = $p \leq 0.05$; ^d = $p \leq 0.1$.

for laboratory analysis of turbidity, suspended solids, nitrate, ammonia, and total phosphorus were collected in acid-rinsed, polyethylene bottles from the same enclosures. One sample was assayed in the lab for turbidity with a HACH turbidimeter (Model 2100A), while the other sample was acidified to pH 2 with concentrated H₂SO₄, stored at 5 °C, and later used for analysis of total phosphorus (TP as PO₄-P), ammonia (NH₄-N), and nitrate (NO₃-N). TP was determined by use of ascorbic acid reduction after digestion with a 5% potassium persulfate solution at 121 °C (15 PSI) for 30 min in an autoclave (Lind, 1985). The phenol/hypochlorite method was used for assay of NH₄-N (Lind, 1985). A modified cadmium reduction method, which replaces 1-naphthylamine with a chromotropic acid indicator (HACH, 1984), was used to measure NO₃-N (Lind, 1985).

Differences across time and treatment were examined with two-way analysis of variance (ANOVA) run on Statistical Analysis System software (SAS, 1985). Four approaches were used to assess sedimentation effects on invertebrates. First, sedimentation effects on total invertebrate density, total insect density, and number of insect families were examined. Second, sedimentation effects on invertebrate abundance was assessed for all observed invertebrate orders. Third, sedimentation effect on families of Coleoptera and Diptera were examined because of the large number of identified families belonging to these orders. Fourth, the effect of sedimentation was evaluated for each functional-feeding group. The transformation $y = (x)^{0.5} + (x + 1)^{0.5}$ was used in the analysis of specific taxonomic groups to compensate for data sets

containing counts of zero (Freeman and Tukey, 1959; Streever et al., 1996). Because of the inherent variability of wetland communities (Streever and Portier, 1994) and the relatively small sample size, statistical significance for all ANOVAs was set at the $p = 0.1$ confidence level rather than $P = 0.05$ (for precedence, refer to Richardson et al. (1976) and Neely and Davis (1985)). Bonferonni adjustments were not used in these analyses because these adjustments tend to be too conservative in evaluation of statistical outcomes.

In addition to the analyses of invertebrate response, ANOVAs were used to examine the effects of sedimentation on water chemistry. In these instances, the effect of sedimentation on water quality was explored in two ways. First, data from samples taken within 24 hours after sediment additions were analyzed to determine short-term effects of sediment additions with time, between treatments, and among the interaction of these factors. Second, water data from samples taken directly before each sediment application were similarly analyzed to test for more long-term effects.

Results

Invertebrate response to sedimentation

Taxonomic group response. Water depth in enclosures from which invertebrates were collected averaged between 16 cm in May to conditions when only shallow (1–2 cm) pockets of water existed in late July and August. *Typha* density and biomass in the study enclosures averaged 42.8 culms m⁻² and

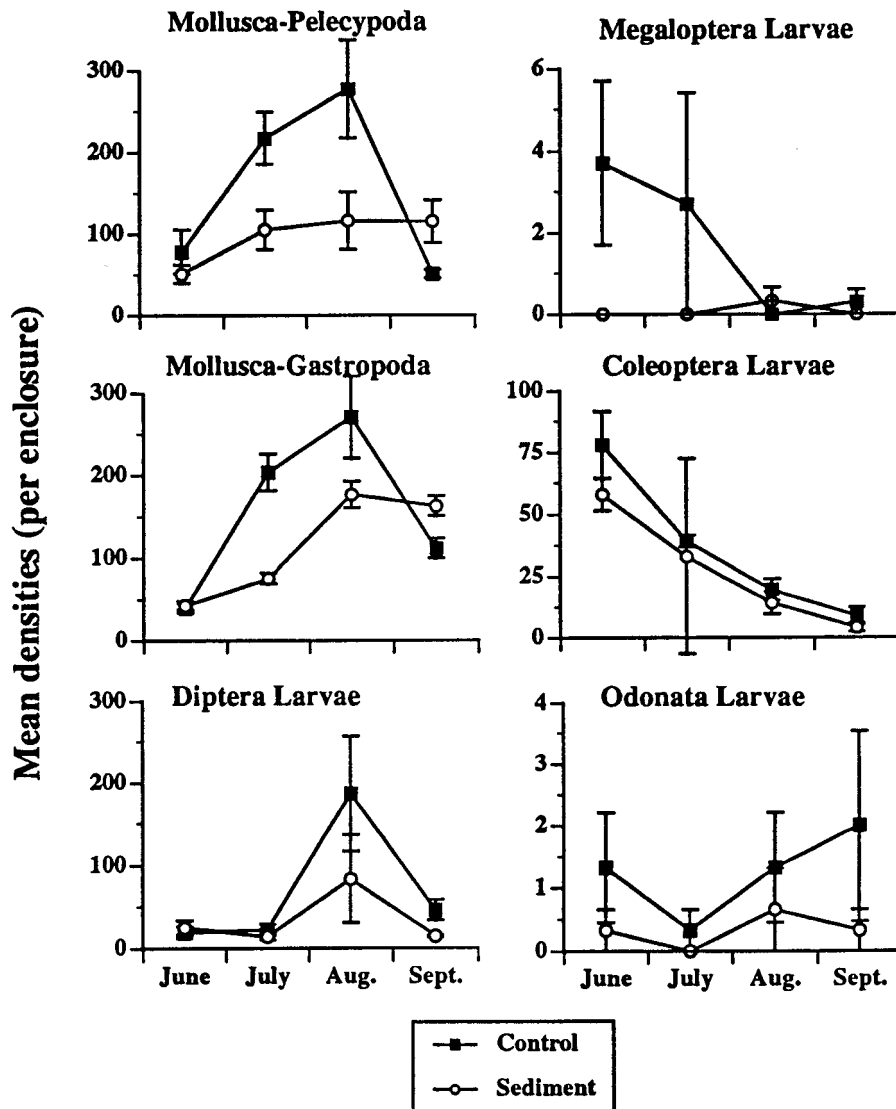


Figure 2. Average density of invertebrate orders significantly affected by sedimentation in experimental enclosures within a *Typha angustifolia* L. wetland at Independence Lake during 1995 (\pm SE, $n = 3$).

2,016.34 g m⁻², respectively. Fourteen invertebrate orders were collected in the enclosures at Independence Lake (Table 1). Total invertebrate density, insect density, and number of insect families were significantly lower in the sedimented enclosures (Table 2 and Figure 1). Although total invertebrate density during the study period averaged 464.2 ± 79.9 (SE) individuals m⁻² in unsedimented enclosures versus 311.4 ± 30.3 individuals m⁻² in sedimented enclosures, the effect of sedimentation was not consistent throughout the study (i.e., significant date \times treatment

interaction-Table 2). The largest difference in invertebrate density occurred between the two treatments in August (Figure 1a); however, total invertebrate density in September was higher in the sedimented treatment plots (Figure 1a). The higher invertebrate density in sedimented enclosures in September resulted only because of the increase in mollusks in those enclosures during September (Figure 2). For the season, insect density averaged 144.2 ± 25.0 individuals in unsedimented enclosures relative to 91.3 ± 14.4 individuals in the sedimented treatment. The largest density differ-

ences between the two treatments occurred in August and September (52% and 57% reductions, respectively – Figure 1b).

For six of the invertebrate orders, either larvae or adults were significantly affected by sediment application (Pelecypoda, Gastropoda, Diptera larvae, Coleoptera larvae, Megaloptera larvae and Odonata larvae – Table 2). For the two mollusk orders, the time \times treatment interaction was also significant (Table 2) because densities were only higher in the unsedimented enclosures during June–August, but not September (Figure 2). Nonetheless, the Pelecypoda (specifically, Sphaeriidae clams) averaged 155.7 ± 32.5 individuals m^{-2} in control enclosures and 96.9 ± 13.6 individuals m^{-2} in the sedimented enclosures for the duration of the study. Similarly, gastropod densities were 156.6 ± 29.0 and 114.8 ± 17.7 individuals m^{-2} in control and sedimented enclosures, respectively.

Larval density in the Coleoptera, Diptera, Megaloptera and Odonata was significantly reduced by sedimentation (Table 2 and Figure 2). The coleopteran larvae were reduced from an average of 36.5 ± 8.5 individuals m^{-2} in control plots to 27.42 ± 6.6 in sedimented areas, a 25% reduction. The effect of sedimentation on dipterans was most evident late in the year (August and September – Figure 2) when densities were approximately 50% lower in sedimented enclosures, relative to unsedimented enclosures. Odonata larvae were consistently lower throughout the growing season in sedimented enclosures, and Megalopterans (specifically, Corydalidae larvae) were virtually eliminated by sediment application; however, the results for these latter two orders should be considered with caution since overall densities were extremely low (Figure 2).

An average of 16 ± 0.8 insect families were observed on each date in the unsedimented enclosures, compared to an average of 13.3 ± 0.7 families observed in the sedimented enclosures (Figure 1c). The largest difference in the number of insect families occurred in September, with 17.0 ± 2.3 families m^{-2} in unsedimented enclosures and 11.0 ± 0.6 m^{-2} in treatment enclosures (Figure 1c). In contrast to total invertebrate density and insect density, the number of insect families did not vary with time throughout the study (Table 2).

Within the order Diptera, the larvae in four families were adversely affected by sedimentation (Table 2). The density of individuals in the Dolichopodidae, Stratiomyidae, Hydrophilidae, and Tabanidae decreased significantly in enclosures exposed to clay

(Table 2 and Figure 3). Only a few individuals of Dolichopodidae were collected during the study in control enclosures (seasonal average = 0.4 ± 0.2 individuals) and none were collected from the sedimented enclosure throughout the study (Figure 3).

For coleopteran families, sedimentation depressed Dytiscidae adults by 53% and Scirtidae larvae by 33% in enclosures receiving clay over the growing season (Table 2 and Figure 3). For these two families, the greatest density differences between the two treatments occurred early in the sampling season and lessened thereafter (Figure 3); however, the date \times treatment interactions were not significant. In contrast, Dytiscidae larval and Carabidae (adult + larvae) densities were initially higher in sedimented enclosures (Figure 3), before declining precipitously in August (significant date \times treatment interaction – Table 2). Dytiscidae larval density and total Carabidae density were approximately three-fold higher in the sedimented enclosures during June and July (Figure 3).

Functional feeding group response. Categorization of collected invertebrates into six functional feeding groups (Table 3) demonstrated significant, sediment-induced effects on the density of three of the six feeding groups (Table 4 and Figure 4): predator-engulfers, collector-filterers, and scrapers. These groups were reduced by 43%, 28% and 27%, respectively, because of clay application. Of these groups, the treatment effect varied with time for the collector-filterers and scrapers (date \times treatment effect – Table 4). In both instances, the interaction presumably resulted from higher numbers of mollusks in sedimented enclosures during September. The gastropods were the largest component of the scraper feeding group, while the pelecypods dominated the collector-filter group.

Of the remaining functional feeding groups, the seasonal pattern of treatment differences suggested that sedimentation also negatively affected the density of predator-piercers and collector-gatherers, particularly late in the growing season (Figure 4). Although these differences were not significant, nearly two-fold differences were evident in August and September.

Summary of effect of sedimentation on water chemistry

Eight measures of water chemistry were conducted biweekly throughout the season in unsedimented and sedimented enclosures. Samples from sedimented enclosures were taken both before and after sediment-

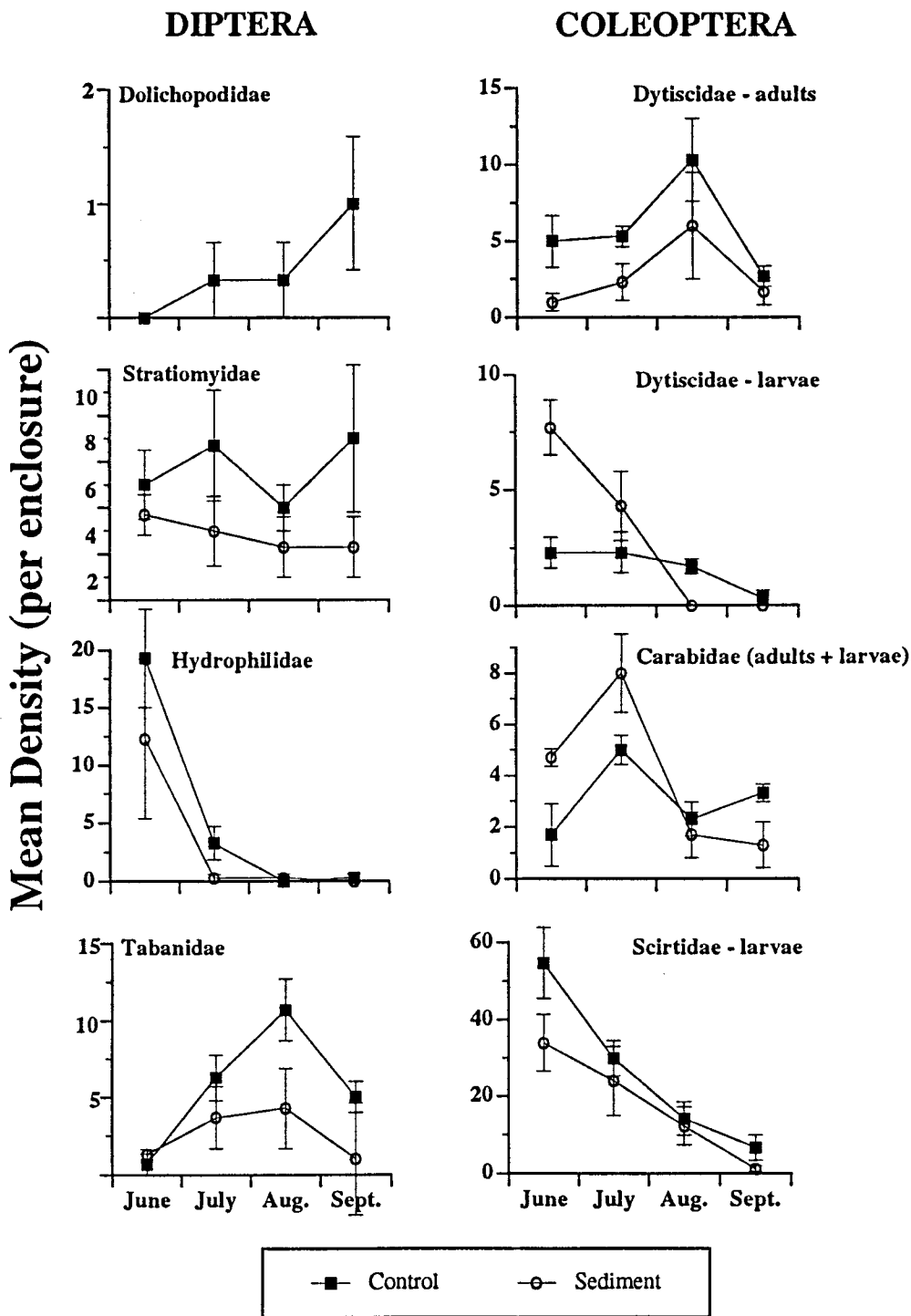


Figure 3. Average density of Dipteran and Coleopteran families significantly affected by sedimentation in experimental enclosures within a *Typha angustifolia* L. wetland at Independence Lake during 1995 (\pm SE, n = 3). Notes: no Dolichopodidae were found in sedimented enclosures throughout the study; adult and larval Coleoptera combined for purposes of presentation.

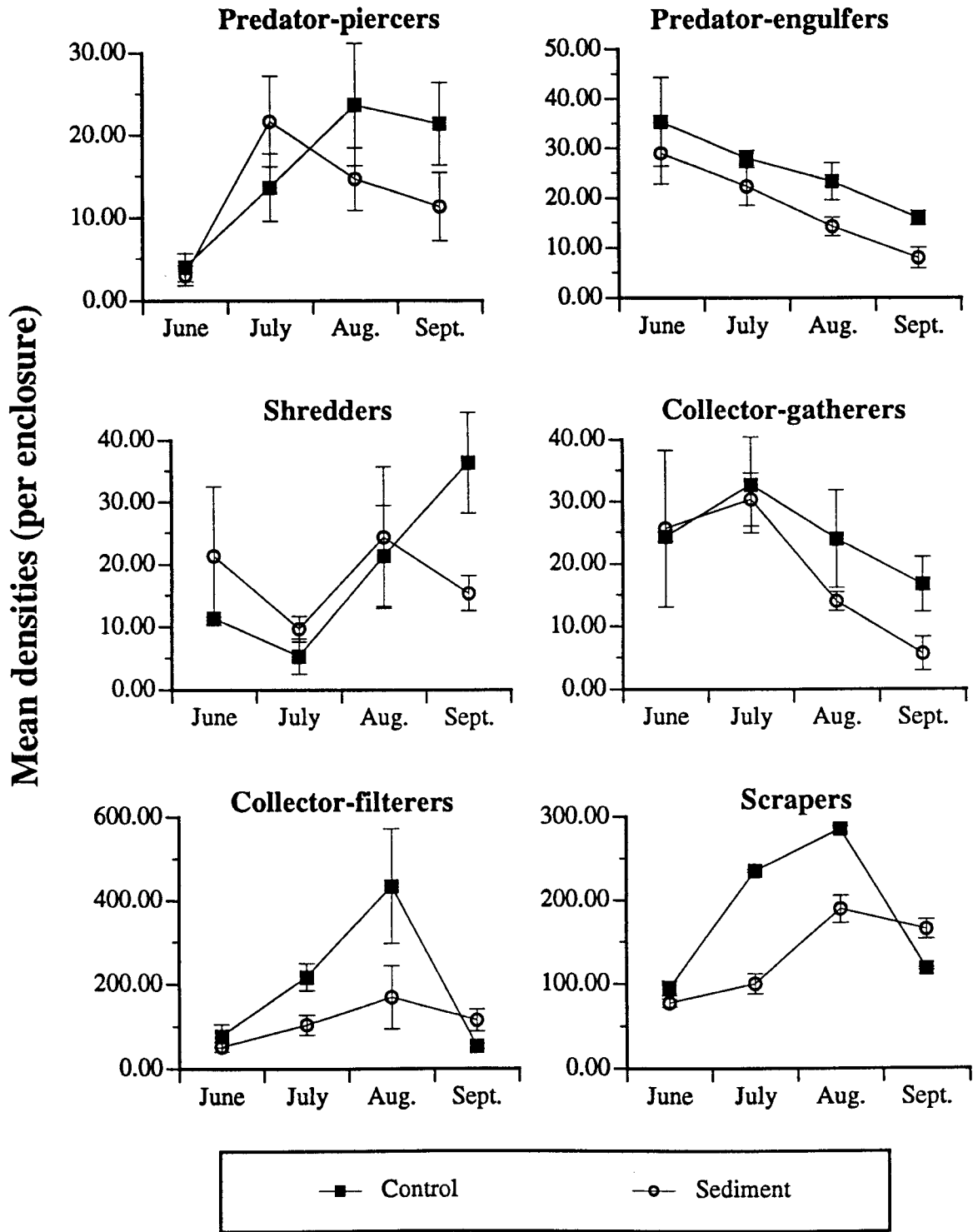


Figure 4. Average density of functional feeding groups collected from experimental enclosures within a *Typha angustifolia* L. wetland at Independence Lake during 1995 (\pm SE, n = 3).

Table 3. Assignment of taxonomic groups collected from experimental enclosures in a *Typha angustifolia* L. wetland at Independence Lake, Michigan, into functional feeding categories.

<i>Predator-piercers</i>
Hemiptera adults and larvae: Belostomatidae, Hebridae, Pleidae, Veliidae
Diptera larvae: Ceratopogonidae, Tabanidae
Coleoptera adults: Histeridae
Hirudinea: Erpobdellidae, Glossiphoniidae
Hydrachnellae
<i>Predator-engulfers</i>
Diptera larvae: Dolichopodidae, Empididae, Sciomyzidae
Megaloptera larvae: Corydalidae
Coleoptera larvae: Carabidae, Dytiscidae, Hydrophilidae, Lampyridae, Staphylinidae
Coleoptera adults: Carabidae, Dytiscidae, Staphylinidae
Odonata larvae: Aeshnidae, Coenagrionidae, Libellulidae
<i>Collector-filterers</i>
Diptera larvae: Culicidae
Pelecypoda: Sphaeriidae
<i>Collector-gatherers</i>
Diptera larvae: Chironomidae, Ptychopteridae, Stratiomyidae, Syrphidae
Coleoptera adults: Hydrophilidae
Ephemeroptera larvae: Baetidae
Collembola: Entomobryidae
Oligochaeta
<i>Shredders</i>
Diptera larvae: Ephydriidae, Tipulidae
Coleoptera larvae: Haliplidae
Coleoptera adults: Anthicidae, Curculionidae, Haliplidae, Scirtidae
Lepidoptera larvae: Noctuidae, Tortricidae
<i>Scrapers</i>
Coleoptera larvae: Scirtidae
Coleoptera adults: Hydraenidae
Gastropoda

ation events to ascertain the long-term versus short-term effects of sedimentation, respectively (Table 5). On a long-term basis, only turbidity, suspended solids and pH were significantly altered by sediment application (Table 5). Turbidity levels averaged approximately four-fold higher in samples taken in sedimented enclosures prior to each sediment application (12.5 ± 3.3 versus 2.8 ± 0.4 nephelometric turbidity units – NTUs) (Table 5), but averaged as high as 59.1 ± 11.3 (SE) NTUs in sedimented enclosures in the 24 hours after sediment was applied, i.e., about 21-fold higher

than the average in control enclosures. Thus, turbidity was continuously elevated in the sedimented enclosures, but, as expected, maximum values were observed immediately after sedimentation. Increases in suspended solid concentrations between the two treatments paralleled the turbidity differences. Suspended solids differed markedly in the first 24 hrs after clay application, averaging 0.92 ± 0.08 mg l⁻¹ in the sedimented enclosures relative to 0.28 ± 0.48 mg l⁻¹ in unsedimented, control enclosures. Similarly, samples taken before sediment application demonstrated that total

Table 4. Degrees of freedom, F-value and statistical significance for ANOVAs comparing density of family members in the Coleoptera and Diptera collected from sedimented and unsedimented enclosures in a *Typha angustifolia* L. marsh at Independence Lake in 1995 (only those with significant treatment differences are listed*).

EFFECT	d.f.	Coleoptera				Diptera			
		Dytiscidae – adults	Dytiscidae – larvae	Carabidae – larvae	Scirtidae – larvae	Dolichopodidae	Stratiomyidae	Syrphidae	Tabanidae
Date	3	4.35 ^c	16.06 ^a	6.95 ^b	16.73 ^a	1.27	0.35	0.71	3.91 ^c
Treatment	1	5.80 ^c	5.69 ^c	3.37 ^d	3.93 ^d	5.00 ^c	4.92 ^c	3.46 ^d	4.80 ^c
Date*Treatment	3	0.34	7.53 ^b	1.12	0.94	1.27	0.39	1.25	1.08

* Families not significantly affected by treatment: Diptera larvae – Ceratopogonidae, Chironomidae, Culicidae, Empididae, Ephydriidae, Ptychopteridae, Sciomyzidae, Tanyderidae, Tipulidae; Coleoptera (adults unless noted otherwise) – Haliplidae larvae, Hydrophilidae larvae, Lampyridae larvae, Staphylinidae larvae, Anthicidae, Scirtidae, Carabidae, Curculionidae, Dryopidae, Haliplidae, Histeridae, Hydraenidae, Hydrophilidae, Staphylinidae.

^a = $p \leq 0.001$; ^b = $p \leq 0.01$; ^c = $p \leq 0.05$; ^d = $p \leq 0.1$.

Table 5. Seasonal averages (\pm SE) of various water quality parameters from experimental enclosures within a *Typha angustifolia* L. wetland at Independence Lake, Michigan, during the 1995 growing season. Water samples were taken from sedimented enclosures both before and within 24 hours after sediment application.

Parameter	n	Control enclosures	Sedimented enclosures	
			Before application	After application
pH*	23	7.49 \pm 0.06	7.38 \pm 0.08	7.38 \pm 0.09
Turbidity* (NTUs ^a)	23	2.75 \pm 0.43	12.48 \pm 3.26	59.09 \pm 11.31
Suspended solids** (mg/l)	23	0.34 \pm 0.12	0.61 \pm 0.21	0.91 \pm 0.49
Dissolved O ₂ (mg/l)	23	0.53 \pm 0.03	0.52 \pm 0.03	0.62 \pm 0.07
NO ₃ -N (mg/l)	23	0.01 \pm 0.004	0.01 \pm 0.004	0.02 \pm 0.004
NH ₃ -N (mg/l)	23	0.50 \pm 0.20	0.66 \pm 0.14	0.34 \pm 0.09
Total P as PO ₄ -P (mg/l)	23	0.56 \pm 0.12	0.62 \pm 0.13	0.37 \pm 0.07

* Significant difference between control and 'before sedimentation' enclosures ($p \leq 0.05$).

** Significant difference between control and 'before sedimentation' enclosures ($p \leq 0.1$).

^a NTU = nephelometric turbidity unit.

suspended solids were continuously elevated in the sediment enclosures (0.61 ± 0.27 mg l⁻¹ in treatment enclosures versus 0.34 ± 0.15 mg l⁻¹ in the control enclosures). All differences in suspended solids were statistically significant over the growing season (Table 5). Sedimentation also significantly reduced the pH of the water column in enclosures by a small amount. The average pH in control enclosures was 7.49 ± 0.06 , relative to 7.38 ± 0.08 in the sedimented plots over the season (Table 5). No immediate effect of sedimentation on pH was noted (Table 5).

Total phosphorus also was affected by sedimentation, but only in the first 24 hrs after sediment application. TP concentrations during the first 24 hours after clay application were significantly lower in enclosures receiving clay relative to the unsedimented treatment,

i.e., in control enclosures, concentrations averaged 0.56 ± 0.13 mg l⁻¹ as opposed to 0.37 ± 0.07 mg l⁻¹ in sedimented enclosures during the first 24 hours after sedimentation (Table 5). Over the course of the season, however, TP concentrations were not significantly different between the two treatments (Table 5).

Discussion

The ability to retain sediments is inherent to the nature of wetlands. Typical values of sedimentation range from about 0.5 cm yr⁻¹ to greater than 3–4 cm yr⁻¹ (Johnston et al., 1984; Fennessey et al., 1994), much higher than the sedimentation rates used in this study. Reduced rates of water flow and substantial vegeta-

tion cause sediments to be deposited over the wetland substrata. This function is recognized, and often exploited, by humankind without adequate information regarding the response of both flora and fauna in wetlands exposed to sedimentation. The literature clearly shows that sedimentation negatively impacts the density (Nuttall and Bielby, 1973; Wagener and LaPerriere, 1985; Quinn et al., 1992) and taxonomic richness (Lenat, 1984; Quinn et al., 1992) of many invertebrate groups in lotic communities. Little reason exists to expect that invertebrate communities in wetland habitats are less sensitive to sedimentation. In fact, sediment deposition may more severely affect lentic invertebrates than lotic organisms. In rivers and streams, some habitats may be resistant to sediment deposition due to constant scouring or continual resuspension of particulate matter by flowing water; in addition, the invertebrate community can drift downstream to escape the burial effects (Culp et al., 1986). However, in wetlands, stagnant conditions hinder re-suspension and removal of sediment as well as invertebrate relocation.

The data from this study at Independence Lake clearly show that the wetland invertebrate population density in general, and some specific taxonomic groups, were negatively affected by sedimentation in a manner analogous to those found in studies of rivers and streams. Suppression of total invertebrate density, total insect density, and the number of insect families by clay sedimentation was not unexpected. These results are consistent with sediment-induced alterations to invertebrate density and biomass in lotic habitats (Nuttall and Bielby, 1973; Lenat, 1984; Wagener and LaPerriere, 1985; Quinn et al., 1992). On the other hand, the small number of taxonomic groups specifically affected by sedimentation was surprising (only four of the fourteen orders collected and a few specific families in the Diptera and Coleoptera – Figures 3 and 4). In part, the absence of statistical differences for many groups probably resulted from the low and variable numbers of individuals collected in those groups (e.g., Streever et al. (1996) discuss the low statistical power of such studies). The absence of statistical differences, however, may also indicate that other stressors in wetland habitats affect invertebrate communities in a more prevalent way than sedimentation, e.g., oxygen regimes in both the control and sedimented enclosures were essentially anaerobic (approximately 0.5 mg l^{-1} – Table 5).

The observations that some specific taxonomic groups were affected by sedimentation also suggests that not all wetland invertebrate groups may be af-

ected by sediment-associated stress in the same way. At the level of order, the Lepidoptera, Oligochaetes, and Hirudinea seemed relatively unaffected. Differences in ability to cope with disturbance are a fundamental aspect of life-history theory, but illustrate the need for more detailed information of wetland invertebrates at the species-specific level. For example, Dittmar and Neely (1999), in a sedimentation study involving wetland vegetation, found that plant responses could only be understood in the context of species life-history strategies. In addition to taxon-specific differences, the stage of maturation may be a significant determinant of invertebrate response to sedimentation, with larvae demonstrating greater susceptibility to sedimentation in some taxonomic groups (Megaloptera and Coleoptera – Figure 2). Cordone and Kelley (1961) reported similar observations in which adult invertebrates in streams seemed more tolerant of high levels of suspended solids. Thus, without detailed information for mature and immature individuals of different species, prediction of sedimentation effects on wetland invertebrates will be difficult.

These generalizations are equally true of the invertebrates in a functional context, i.e., sedimentation did not affect all functional feeding groups. Predator-engulfers, collector-filterers, and scrapers were adversely affected by sediment additions (Figure 4). In the predator-engulfers, the bottom-dwelling Dolichopodidae larvae (Diptera) and free-swimming Dytiscidae adults (Coleoptera) were two groups particularly adversely affected by sedimentation. Such declines might seem intuitive because of sediment-induced decreases in prey or decreased visual ability because of high turbidity levels. In contrast, however, densities of two other predator-engulfers (Carabidae and Dytiscidae larvae) seemed to increase in sedimented enclosures. Although these latter differences were only significant at the 0.1 confidence level, they nonetheless demonstrate the complexity of predicting how wetland invertebrates might respond to sedimentation. Perhaps the decline in some predator-engulfers resulted in competitive release, thereby allowing other predator-engulfer taxa to flourish.

Culicidae (mosquito larvae) and pelecypods were the only filter-feeders identified in this study. Again, this feeding-group also illustrated the difficulty in predicting overall sedimentation effects. The statistically significant inhibition of collector-filterers by sedimentation was primarily related to the significant decline in numbers of Pelecypoda because the culicids were relatively unaffected. The multivoline

nature of culicids (i.e., continual recruitment) (Merritt and Cummins, 1996) may have minimized treatment effects within this group.

The scraper functional-feeding group exhibited the most uniform response to sedimentation (Figure 4). Such declines are likely attributable to declines in periphyton biomass available for consumption, either because of burial or lower periphytic productivity. Graham (1990) found that silt accumulation reduced the organic content of epilithic periphyton to only 22% of dry biomass (compared to 52% in a control stream). Similarly, Davies-Colley et al. (1992) found that after clay discharges in streams, the reduction in light (from an increase in turbidity) also caused a significant reduction in benthic primary productivity, reducing the quantity and/or quality of food available for scrapers.

Although this study was not designed to determine the precise mechanism or cause through which sedimentation affects invertebrates, it is obvious that both direct and indirect mechanisms may be involved. Probable direct mechanisms include burial of food sources or interference with feeding structures whereas indirect mechanisms primarily manifest themselves through changes in water chemistry. Davies-Colley et al. (1992) listed five possible mechanisms for the deleterious effects of clay discharges on stream organisms: (1) reduced light penetration in turbid water which reduces primary production; (2) reduced quality of epilithon as food for invertebrates; (3) filling of invertebrate niche (habitat) space; (4) avoidance of sedimented areas by invertebrates, fish, and aquatic birds; and (5) accumulation of sediment particles on invertebrate body surfaces and respiratory structures.

Most notably, both turbidity and the mass of suspended solids in the water column were significantly elevated in sedimented enclosures. Turbidity and suspended solids were not only higher in sedimented enclosures during the first 24 hours after sedimentation, but were also consistently elevated throughout the growing season. These results were not unexpected and are typical of sedimentation studies in other aquatic systems (Gray and Ward, 1982; Wagener and LaPerriere, 1985; Davies-Colley et al., 1992). In a study of the effects of clay discharges from mines on stream systems, Quinn et al. (1992) reported that turbidity increased by 7–154 NTU above normal mean values of 1.3–8.2 NTU. Furthermore, suspended solids also increased and exhibited a strong positive correlation with turbidity (Quinn et al., 1992). Turbidity and suspended solids are obviously indices of particulate

matter which must eventually settle at the sediment-water interface. At Independence Lake, clay accumulation on the vegetation and detritus was clearly evident in the sedimented enclosures and undoubtedly resulted in the burial of some invertebrates, their habitat, and potential food supplies. Although definitive conclusions are not possible, a logical assumption is that burial of organisms and their resources were the primary reasons for the observed declines in some of the invertebrate groups.

To a lesser extent, the invertebrates may have been suppressed by changes in other water quality parameters; however, pH was the only other variable significantly altered by the sediment treatment. Lemly (1982) also reported lower pH regimes at the interface of substrate and water in a stream following sediment additions (a maximum difference of 0.9 pH units). Although the small pH differences between the treatments at Independence Lake seem unlikely to have been great enough to have excluded specific taxa, increased acidity has been shown to affect organisms and various processes in aquatic ecosystems. In streams with a pH below 4.0, Hall et al. (1980) found declines in total benthic macroinvertebrate density emergence of adult insects (including some dipterans) and adult collectors. Other work has demonstrated that acidity, coupled with aluminum toxicity, alters respiration rates in dragonflies (Rockwood et al., 1990) and mayflies (Herrmann and Andersson, 1986).

Although total phosphorus concentrations were not suppressed in sedimented enclosures for the entire summer, an immediate decline in TP in the treatment enclosures after sediment application did occur, i.e., a 34% decline in sedimented enclosures immediately after sedimentation events. Clay particles are highly reactive and known to bind with other compounds; thus, phosphorus was undoubtedly removed from the water column as the clay particles settled (both $\text{PO}_4\text{-P}$ and dissolved organic carbon decline immediately after clay application in samples from Independence Lake – Neely, unpublished data). Although no form of phosphorus is directly absorbed by macroinvertebrates, the growth of the periphyton upon which some invertebrates feed is often limited by available phosphorus (Roos, 1983). For example, Quinn et al. (1992) found invertebrate densities to be significantly lower downstream of clay discharge areas presumably because of lower epilithon (periphyton) biomass as well as degraded food quality. Thus, changes in water chemistry may exhibit an indirect effect on macroinvertebrates via alteration of food resources.

In summary, this study illustrates that the macroinvertebrate fauna of wetlands, at the broadest taxonomic levels, can be altered by sedimentation events. Overall reduction in invertebrate numbers are particularly important in a food-chain context in which waterfowl and other vertebrates use wetland macroinvertebrates as a protein source. The impact of sedimentation, however, was not uniform across all invertebrate orders and families. The magnitude of such variability is likely to be even larger for lower taxonomic levels. Similarly, taxonomic groups will undoubtedly differ in their individual ability to cope with sedimentation varying in texture, organic content, and loading regime. Within a single wetland, such sedimentation differences are probable whereby coarse particles fall from suspension near inflows while finer particles, such as clay, are carried further into the wetland before deposition, i.e., a depositional texture gradient. An understanding of such depositional patterns and concomitant organismal effects is needed to ascertain the consequences of using wetland basins for sediment retention.

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