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Relationships between environmental characteristics and macroinvertebrate communities in seasonal woodland ponds of Minnesota

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Abstract. We related macroinvertebrate communities and environmental variables in 66 small seasonal woodland ponds of northern Minnesota, USA. These wetlands were relatively pristine, being embedded in 50- to 100-y-old 2nd-growth forests. Macroinvertebrate taxon richness in ponds increased as hydroperiods lengthened, tree canopies opened, water pH declined, and litter input decreased. Eighteen macroinvertebrate taxa were widespread (occurred in >50% of ponds), and hydrology, water chemistry, geomorphology, vegetation, occurrence of other macroinvertebrate taxa, and presence of amphibian larvae each explained some variation in relative abundance of widespread macroinvertebrates. The first 4 axes of a canonical correspondence analysis explained 37% of total variation in relative abundance of widespread macroinvertebrate taxa. Overall, however, macroinvertebrates were remarkably unresponsive to environmental variables. Most relationships between macroinvertebrates and environmental variables were nonsignificant, and the few significant relationships observed were weak (<20% of variation). We suggest that this lack of response occurs because most macroinvertebrates in seasonal woodland ponds are habitat generalists. These species routinely endure pronounced and unpredictable environmental changes; hence, they possess a durability that makes them resistant to most natural variation in habitat conditions.

Key words: wetlands, invertebrates, hydroperiod, canopy cover.

There are several hypotheses about ecological controls on macroinvertebrate communities in seasonal ponds. The treatise by Wiggins et al. (1980) on seasonal ponds in Ontario focused attention on hydroperiod, and maintained that drying prevented many organisms from exploiting these temporary habitats. Recent studies by Schneider and Frost (1996) in 7 Wisconsin ponds, Brooks (2000) in 5 Massachusetts ponds, and Fairchild et al. (2003) in 9 Pennsylvania ponds contrasted invertebrate communities along a hydroperiod gradient, and reported that faunas from ephemeral habitats were different from those in permanent ponds. However, in a more extensive study of 41 ponds in Colorado, Wissinger et al. (1999) found little evidence that hydrology directly affected community structure beyond the fact that only a few invertebrates exploited extremely short-duration ponds. Wissinger et al. (1999) suggested that the most important influence of hydroperiod was indirect, with hydrology affecting distributions of predaceous salamanders, which in turn affected invertebrate abundance. Few would argue that wetland organisms must deal effectively with temporary drying, but Williams (1996) suggested that drying is not a difficult barrier to overcome because the ability to survive dry periods has evolved repeatedly in a wide range of unrelated wetland taxa. For species adapted to seasonal wetlands, drying may not be a major environmental constraint.

Wetland ecologists have tacitly assumed that water chemistry is an important influence on wetland invertebrates (Batzer and Wissinger 1996), although little quantitative evidence exists to support this hypothesis. In semi-arid western Australia, Growns et al. (1992) found that invertebrate communities varied with water color and nutrient concentration. Nutrient levels also limited invertebrates in an oligotrophic marsh in Canada (Campeau et al. 1994, Gabor et al. 1994). In some North American prairie wetlands, highly saline or alkaline conditions permit only the most tolerant organisms to per-

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sist (Euliss et al. 1999, Lovvorn et al. 1999). However, each of these wetlands showed extreme (high or low) chemical concentrations, which in some cases were anthropogenically induced. Examples of associations between water quality and invertebrates from natural habitats with more moderate chemistries appear to be lacking (Batzer and Wissinger 1996, Wissinger et al. 1999, Battle and Golladay 2001).

The hydrology and water chemistry of seasonal ponds both are undoubtedly governed by landscape features, so one might expect macroinvertebrate communities to vary with changes in landscape characteristics, such as landform or soil type. However, limited information exists on how macroinvertebrates in seasonal ponds are influenced by landscape features (Euliss et al. 1999, Hall et al. 1999). Some authors have speculated that patch size influences biotic diversity of seasonal ponds (Ebert and Balko 1987, Hall et al. 1999, Wissinger et al. 1999), so macroinvertebrate communities may vary with pond size.

In addition to abiotic factors, biotic features also may influence invertebrates in seasonal woodland ponds. Recent evidence suggests that, like streams (Wallace et al. 1997), the condition of the surrounding upland forest and litter input influence macroinvertebrate communities in ponds (Higgins and Merritt 1999, Batzer et al. 2000, Palik et al. 2001). Entrekin et al. (2001) and Battle and Golladay (2001) hypothesized that differences in plant communities among ponds affect distributions of wetland invertebrates by altering food quantity and quality. In addition to bottom-up trophic influences with plants, macroinvertebrates in seasonal ponds also may be controlled by predation (Wellborn et al. 1996, Wilbur 1997, Wissinger et al. 1999). Most research in seasonal ponds has focused on invertebrate predation by vertebrates (see reviews by Batzer and Wissinger 1996, Wissinger 1999), whereas the importance of predaceous macroinvertebrates has not been evaluated (but see Higgins and Merritt 1999, Battle and Golladay 2001).

With the possible exception of hydrology, there is little compelling evidence to support any hypotheses regarding controls on macroinvertebrates in seasonal ponds. Very few studies have addressed any particular hypothesis, and most published studies have been conducted on a small number of sites (<10). Attempts to test competing hypotheses are even rarer (but see Wissinger et al. 1999). The goal of our study is to describe macroinvertebrate communities and habitat conditions in a large set of seasonal woodland ponds in Minnesota, USA, and to determine how much variation in composition is explained by various abiotic and biotic habitat factors. We also provide a correlative means of testing and comparing some of the emerging hypotheses regarding the maintenance of macroinvertebrate communities within seasonal ponds.

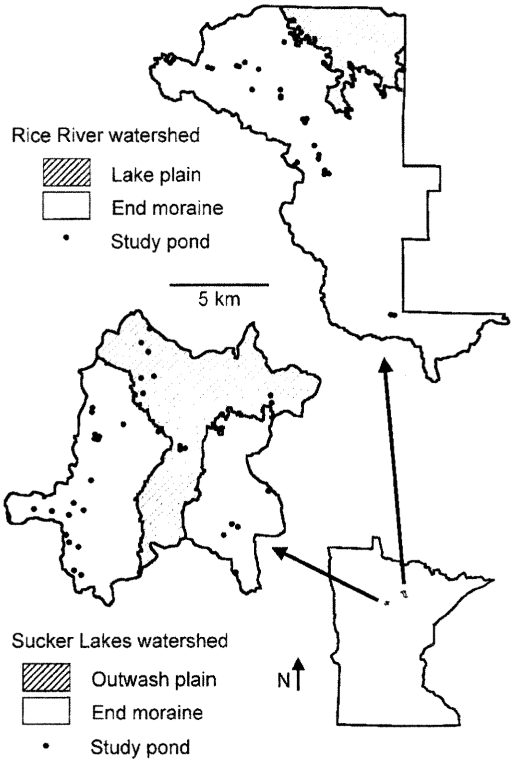

FIG. 1. Locations of the Sucker Lakes (lat 47°15′N, long 94°30′W) and Rice River (lat 47°45′N, long 93°37′W) watersheds in northern Minnesota's Chippewa National Forest.

Methods

Study watersheds and pond selection

We conducted our study on the Chippewa National Forest in north-central Minnesota within the Sucker Lakes and Rice River watersheds (Fig. 1). Dominant glacial landforms included ground moraine and outwash plain in the Sucker Lakes watershed and end moraine and lake plain in the Rice River watershed. Upland forests within study watersheds were mostly mixed pines (*Pinus banksiana, P. resinosa,* and/or *P. strobus*) on the outwash, and mixed hardwoods (*Populus tremuloides, P. grandidentata, Acer saccharum, Tilia americana,* and/or *Quercus rubra*) on the moraines and lake plain. Glacial landforms were mapped as part of the National Forest's ecological classification and inventory (Chippewa National Forest 1996). In addition, National Forest personnel identified and digitized all seasonal ponds in study watersheds using 1:24,000 leaf-off color-infrared air photography.

We randomly selected 66 ponds for study in 4 glacial landforms (Fig. 1). We constrained our selection of ponds using the following criteria: 1) the surrounding forest was >50 y old; 2) ponds and surrounding forests showed no evidence of recent disturbance; 3) pond area was >0.02 but <0.5 ha; 4) ponds had mineral or mixed mineral and organic soil substrates, as opposed to peat; and 5) water depth in pond basins at the time of selection in spring 1997 was >15 cm. In total, we selected 25 ponds in the ground moraine, 12 ponds in the outwash plain, 25 ponds in the end moraine, and 4 ponds in the lake plain.

Sampling

Hydrology.—We measured water depths in each pond using a metal staff gage placed in the deepest part of each basin. We read gages weekly to biweekly between 1 April and 30 September 1998 and 1999, sampling all 66 ponds within 1 or 2 d. Ponds in the Sucker Lakes watershed also were monitored in 1997.

Water chemistry.—We collected water samples from each pond, if they held water, on the same dates we read staff gages. We stored unfiltered water at 4°C in 0.5-L polyethylene bottles for a maximum of 30 d before analysis. We measured pH (Corning model 440 meter and Orion 8102 electrode), conductivity (YSI Model-35), and alkalinity (autotitration to pH 4.5, Mettler DL20 titrator followed by Gran plot analysis). We determined NO_3-N (detectable to 0.02 mg/L), NH_4-N (0.02 mg/L), total N (0.02 mg/L), and total P (0.5 mg/L) by colorimetric procedures on a Lachet Quik Chem 8000 flow-injection system, with inline persulfate digestion for total N and total P. Total organic C was measured using a Dorhmann DC-190 analyzer. We measured color (as absorbance) of water samples using a Spectronic 21D.

Pond size.—We determined pond surface area using the seasonal high-water level in 1998. Presence of high-water marks, such as sediment-coated or recently saturated leaf litter, was used to establish pond margins. We measured margin-to-margin pond length in 2 perpendicular dimensions, and used those dimensions to estimate surface area using the formula for an ellipse.

Vegetation.—In 1998 in each pond, we established 1 line transect that spanned the basin's longitudinal axis, and recorded herbaceous plant cover and coarse woody debris (CWD) along the transect using the line-intercept method. We defined CWD as trunks and branches >5 cm diameter at their narrowest point within the pond basin. We assigned plant cover, as a distance along the transect, to categories including sedge, grass, floating-leaved plants, submersed plants, or bryophytes.

In each pond, we sampled woody vegetation in 5.6-m radius circular plots centered on 3 equidistant points on the transect line; in some small ponds we could only establish 1 or 2 points. In each plot, we recorded the species and diameter at 1.4 m height of each tree ≥10 cm. In mid-summer we estimated pond overstory canopy cover above the shrub layer using a spherical densiometer. Ponds were small so densiometer readings reflected canopy cover over the basin and the upland forest adjacent to ponds. In 1998, we placed 1 or 2 litter traps in each basin, depending on pond size, to estimate input of coarse particulate organic matter (CPOM). We collected litter monthly from May through early September and then biweekly until early November, with a final collection in early spring 1999. We dried litter at 65°C for 48 h and then weighed it (nearest 0.1 g) to determine dry mass.

Macroinvertebrates.—We sampled macroinvertebrate assemblages in each of the 66 ponds while they held water in 1998 and 1999. We sampled in mid May to collect the spring fauna and again in late June to collect later colonizers. We used a D-frame net (30 cm width, 1 mm mesh) because it samples macroinvertebrate communities from wetlands efficiently and precisely (Cheal et al. 1993, Batzer et al. 2001). The net mesh was small enough to retain most invertebrates but large enough to prevent excessive clogging by fine sediments (Batzer et al. 2001). During each sampling visit, we used three 1-m long sweeps, the 1st near the pond edge, the 2nd in the pond center, and the 3rd either at a halfway point between the edge and center or in a subhabitat (e.g., in emergent plant stands, woody debris) that otherwise was not sampled in the first 2 sweeps. Wetted areas varied among ponds and changed temporally, although we did not weight our sampling effort by area. We scraped the net horizontally along the pond bottom to collect both benthic and free-swimming organisms. Contents of the 3 sweeps were pooled into 1 composite sample per pond, and the collected material was preserved with 95% ethanol. In the laboratory, we separated macroinvertebrates from mud and detritus by hand and identified them to family or genus using Pennak (1989), Thorp and Covich (1991), and Merritt and Cummins (1996). We expressed relative abundance of macroinvertebrates per pond sample, encompassing ~0.9 m^2 of wetted habitat.

Amphibians.—We used dipnets and funnel traps to sample amphibian (frog and salamander) larvae. We conducted dip netting from late May to early June in 1998 and 1999, a time when larvae were identifiable to species. For each pond, we used a time-constrained search in which 2 people swept the water for 15 min. We held captured amphibians in buckets until the end of the sampling period, and then identified and released them. We used hardware-cloth (6 mm mesh) funnel traps to sample larvae from 3 June to 9 July. We used either 2, 4, or 6 unbaited traps per pond, depending on pond size. We spaced traps evenly across ponds, perpendicular to shore, in water deep enough to submerge most of the trap yet provide an air space for adult amphibian respiration. We checked traps daily for 3 d. We identified trapped amphibians to species and released them.

Statistical analyses

Macroinvertebrate measures.—We used richness and relative abundance of the most common taxa to assess macroinvertebrate relationships with habitat variation. For richness, we determined the total number of families collected from each pond over the 2-y study. We used families rather than genera for richness analyses because we lacked the expertise or budget to quantify and classify all invertebrates to genus (e.g., Ceratopogonidae, early instar Chironomidae, Ostracoda). For relative abundance, we restricted our analysis to those families collected in >50% of the ponds (= widespread taxa); inclusion of less-widespread taxa with a large number of 0 abundance values would have compromised analyses. We generated composite macroinvertebrate values for each pond by averaging all measurements collected over the 2-y study. However, for some taxa that emerged or diapaused prior to June sampling (i.e., Culicidae, Limnephilidae, Daphniidae), we used only May collections to calculate relative abundance. We could not extrapolate relative abundances to pond abundance because the wetted area of ponds changed throughout the study. Therefore, our measures of basin size did not always reflect availability of aquatic habitat.

Univariate analyses.—We restricted our analyses of hydroperiod to the 183-d span from 1 April through 30 September, a time when ponds were ice free. We estimated hydroperiods by determining cumulative time (d) each pond was flooded. If a pond dried or reflooded, we assumed that the hydrologic transition occurred at the midpoint between monitoring dates. For our 1st hydrologic analysis, we related mean hydroperiods with macroinvertebrates that exploit ponds. We calculated hydroperiod means using only 1998 and 1999 data (1 April–30 September) because in 1997 hydroperiods were measured only in the Sucker Lakes watershed. Two-year mean hydroperiods and macroinvertebrate measures for each pond were related using simple regression. For our 2nd hydrologic analysis, we divided the 66 ponds into 3 equal groups ($n = 22$), with the1st group having the shortest hydroperiods (dry >49 d per summer), the 2nd group having intermediate hydroperiods (dry 29–48 d per summer), and the 3rd group having the longest hydroperiods (dry <28 d per summer). We then contrasted the presence and absence of individual taxa among the 3 hydroperiod groups using χ^2 tests. Hydroperiod changes from year to year, so we conducted a 3rd hydrologic analysis to assess impacts of hydroperiod for a specific year. We regressed taxon richness and relative abundances of widespread taxa in 1998 or 1999 with the hydroperiod of the previous year, reasoning that conditions for reproduction and aestivation by macroinvertebrates the previous year might influence populations the subsequent year. We excluded ponds in the Rice River watershed for the 1998 analysis because 1997 hydroperiod data were not available.

We restricted our analyses of water chemistry to 1998 data because collections were less complete for 1997 and 1999, and chemical conditions in 1998 reflected those in the other years (DPB, unpublished data). We related 1998 mean water chemistry measures to macroinvertebrate variables (2-y composite measures) using simple regression. We also used 1-way ANOVA and a Tukey test to contrast macroinvertebrate measures among the 4 glacial landform types, and a *t*-test to compare macroinvertebrate measures between the 2 watersheds. Macroinvertebrate response measures were related to pond size, canopy cover, sedge cover, CWD cover, tree basal area, and litter input using simple regression. A correlation matrix contrasting patterns of relative abundance among all widespread macroinvertebrate taxa was used to assess interrelationships among taxa. Relative abundance of amphibians was extremely variable from year to year, and quantitative results from dipnetting and funnel traps did not always agree. Therefore, we pooled dipnet and funnel trap data to determine pond-specific presence or absence of amphibians, and we contrasted macroinvertebrate measures between ponds with or without an amphibian species using a *t*-test.

Multivariate analysis.—Abundances of widespread taxa were related to all habitat variables with canonical correspondence analysis (CCA), using CANOCO (C. J. F. ter Braak and A. Smilauer. 1998. CANOCO reference manual and user's guide to CANOCO for Windows: software for canonical community ordination, version 4.0, Microcomputer Power, Ithaca, New York). CCA is a direct gradient analysis that uses multiple regression to develop ordinations that represent taxa distributions constrained by environmental factors such as landform, hydroperiod, canopy cover, etc. We coded categorical variables as a set of dummy variables, one for each category of the variable (i.e., 2 watersheds, 4 landform types). We scored values for individual ponds as either 0 or 1, depending on its occurrence in the category. We used a Monte Carlo permutation test to determine the statistical significance of the relation between species and environmental variables. We performed 2 tests, one based on the 1st canonical eigenvalue and one based on the sum of all canonical eigenvalues. The resulting tests determined the significance of the 1st ordination axis and that of all canonical axes together, respectively. For example, to evaluate the significance of the 1st CCA axis, a *p*-value is computed as $p = (1 + n)/(1 + N)$, where n = the number of randomizations (permutations) with an eigenvalue greater than or equal to the corresponding observed eigenvalue and N = the total number of randomizations (permutations).

α-values and transformations.—We used a critical value of $\alpha = 0.05$ for univariate tests involving taxon richness and the CCA ordination. Bonferroni adjustments of α values for testing multiple variables were unnecessary for univariate tests because we did not hypothesize that richness would respond to every measure (see Perneger 1998). However, for univariate analyses relating relative abundance of individual taxa and environmental variables, we used a more conservative α value of 0.01. We used $\log(x + 1)$ transformations for numerical data and arc sin transformations for % data to meet assumptions of regression and ANOVA. Data were not transformed for CCA.

Results

Faunal composition

Forty-five taxa (families or orders) of aquatic macroinvertebrates were collected from the 66 study ponds (Appendix). Numbers of taxa collected over the 2-y period ranged from 8 to 30 per pond, with some taxa including multiple genera (Appendix). Seventeen families were widespread (occurring in >50% of the habitats; Table 1). The tanypodine Chironomidae were considered as the 18th widespread taxon (78% occurrence) because their mostly predatory behavior makes them ecologically unique from the rest of Chironomidae..

Primary consumers numerically dominated the 18 widespread taxa, including shredders (Limnephilidae, Haliplidae), scrapers (Physidae, Planorbidae, Lymnaeidae), collector-gatherers (non-Tanypodinae Chironomidae, Lumbriculidae, Daphniidae, Culicidae, Cyprididae, Dixidae), and collector-filterers (Sphaeriidae). Predatory beetle larvae and adults (Dytiscidae, Hy-

TABLE 1. Percent occurrences of the 18 most widespread macroinvertebrate taxa (families or subfamilies) in 66 seasonal woodland ponds in northern Minnesota.

Group	% occurrence
Chironomidae (non-Tanypodinae)	100
Lumbriculidae	100
Sphaeriidae	94
Dytiscidae	91
Physidae	89
Chaoboridae	89
Daphniidae	88
Culicidae	82
Limnephilidae	78
Planorbidae	78
Tanypodinae	78
Haliplidae	76
Libellulidae	73
Hydrophillidae	71
Cyprididae	67
Ceratopogonidae	62
Dixidae	61
Lymnaeidae	55

drophilidae), dipterans (Chaoboridae, Tanypodinae, Ceratopogonidae), and dragonfly naiads (Libellulidae) also were widespread and occasionally abundant. Larval wood frogs (*Rana sylvatica*) and blue-spotted salamanders (*Ambystoma laterale*) occurred in 54 and 40 of the 66 ponds, respectively.

Relationships between macroinvertebrates and habitat characteristics

Univariate analyses.—Hydroperiods varied greatly from year to year, with 1998 being the driest summer, 1999 the wettest, and 1997 being intermediate (Fig. 2A). Some ponds were perennially flooded, whereas others were dry for more than half of the sampling period (Fig. 2B). Most ponds that dried reflooded in autumn 1997 and 1999, but 45 of 66 (68%) ponds remained dry in autumn 1998. The total number of macroinvertebrate taxa was positively related to mean hydroperiod ($r^2 = 0.41$, $p < 0.001$, Fig. 3A), largely because glossiphoniids (χ^2 test, $p = 0.004$), erpobdellids ($p < 0.001$), libellulids ($p = 0.002$), limnephilids ($p < 0.0001$), haliplids ($p = 0.002$), tanypodines ($p < 0.001$), and most rare taxa (e.g., leptocerids, pleids) occurred almost exclusively in wetter habitats. In 1999, but not 1998, hydroperiod of the previous year was positively related to taxon richness ($r^2 = 0.11$, $p = 0.009$).

Hydroperiod influenced relative abundances of 4 of the 18 widespread taxa. Mean hydroperiod was positively related to relative abundances of limnephilids ($r^2 = 0.17$, $p = 0.001$), sphaeriids ($r^2 = 0.14$, $p = 0.002$), haliplids ($r^2 = 0.11$, $p = 0.006$), and libellulids ($r^2 = 0.11$, $p = 0.008$). Hydroperiod in 1997 was positively related to relative abundance of limnephilids in 1998 ($r^2 = 0.34$, $p = 0.001$), but hydroperiod in 1998

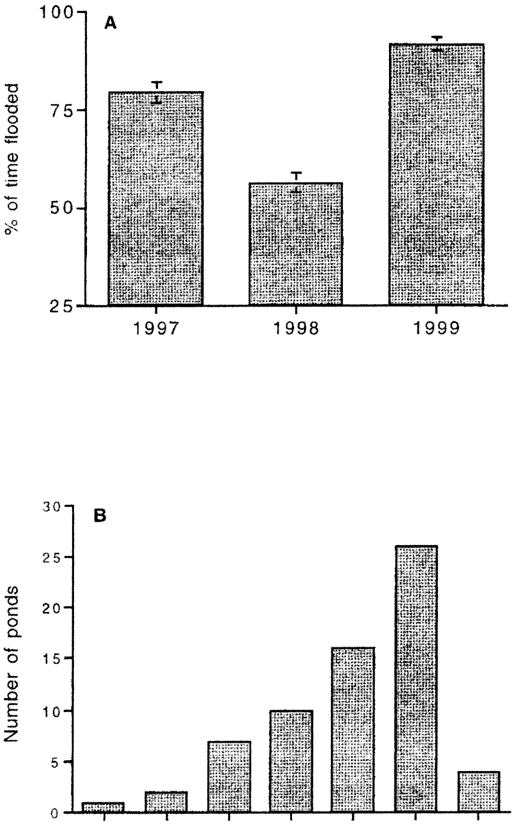

FIG. 2. Mean (±1 SE) annual variation in pond hydroperiod from the 1 April to 30 September (183 d) ice-free period in which ponds held water, during 1997 ($n = 37$), 1998 ($n = 66$), and 1999 ($n = 66$) (A). Statistics for 1997 include only the data from the Sucker Lakes watershed. Percentage of the 1 April to 30 September period in which individual ponds ($n = 66$) held water during 1998 and 1999 (yearly mean for each pond) (B).

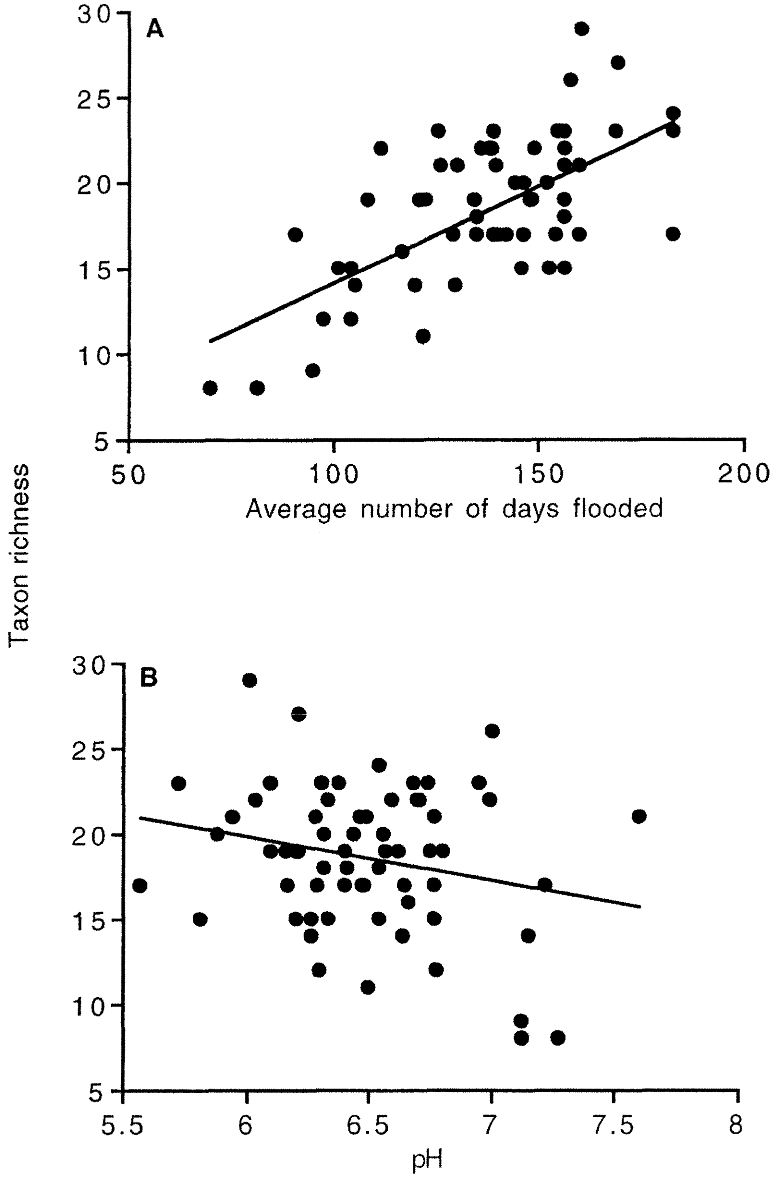

FIG. 3. Associations of macroinvertebrate taxon richness in 66 seasonal woodland ponds with hydroperiod (mean number of days each pond held water from 1 April to 30 September) (A), water pH (B), pond size (C), canopy cover (D), and litter input (E). Taxon richness was defined as the number of aquatic macroinvertebrate families collected over the 2-y study period (1998–1999). Statistically significant relationships ($p < 0.05$) are indicated by regression lines.

was negatively related to limnephilid abundance in 1999 ($r^2 = 0.31$, $p < 0.001$). Hydroperiod in 1998 was positively related to abundance of haliplids in 1999 ($r^2 = 0.14$, $p = 0.002$).

Most water chemistry variables differed among ponds by 1 or 2 orders of magnitude (Table 2). Many of the chemistry variables were interrelated, with strong positive relationships among pH, alkalinity, and conductivity; between total organic C and water color; and among total N, NO_3-N, and NH_4-N ($p < 0.05$). However, variation in macroinvertebrate rich-

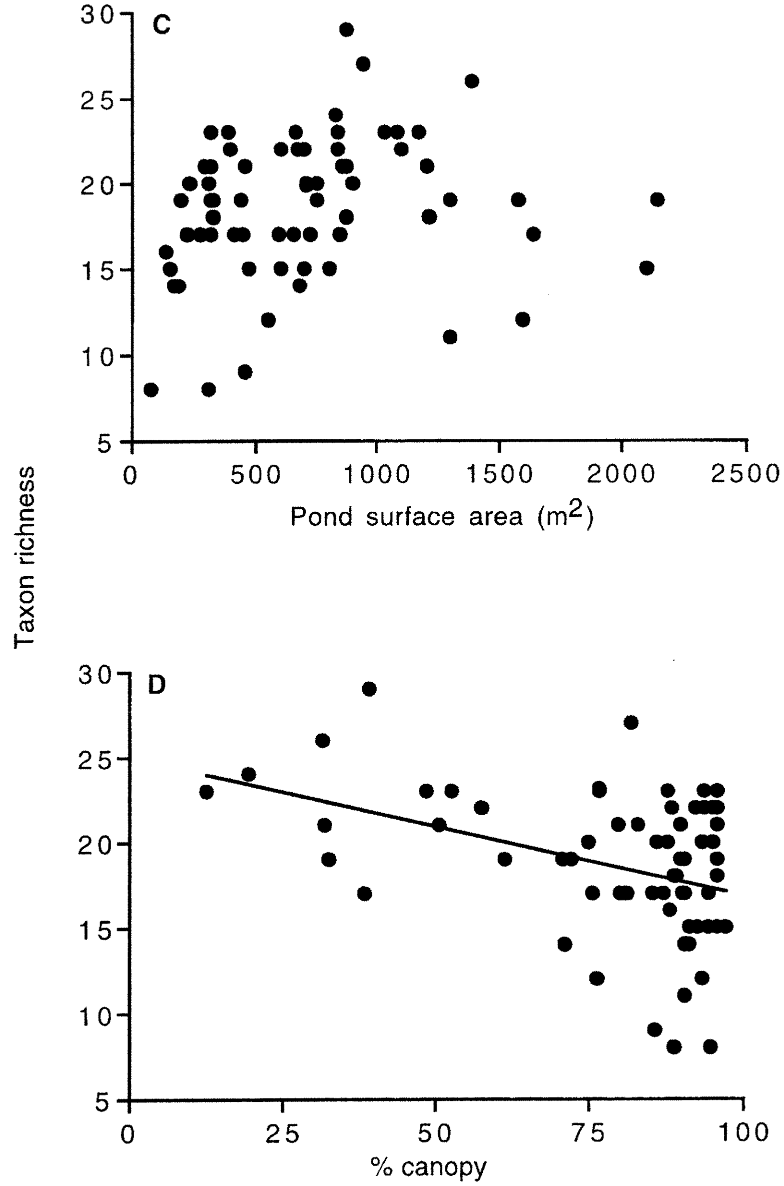

FIG. 3. Continued.

ness or relative abundance was related infrequently to chemical attributes. Macroinvertebrate taxon richness was related to only one chemical variable, pH, and that relationship was weak ($r^2 = 0.06$, $p = 0.051$, Fig. 3B). Limnephilid relative abundance was positively related with alkalinity ($r^2 = 0.35$, $p < 0.001$), conductivity ($r^2 = 0.30$, $p < 0.001$), and pH ($r^2 = 0.17$, $p = 0.001$). Planorbid abundance was positively related with pH ($r^2 = 0.14$, $p = 0.002$), NH_4-N ($r^2 = 0.14$, $p = 0.002$), alkalinity ($r^2 = 0.13$, $p = 0.003$), conductivity ($r^2 = 0.12$, $p = 0.004$), and total N ($r^2 = 0.11$, $p = 0.007$). Both lymnaeid and ostracod abundances were positively related to NH_4-N ($r^2 = 0.23$, $p < 0.001$; $r^2 = 0.22$, $p < 0.001$, respectively) and total N ($r^2 = 0.25$, $p < 0.001$; $r^2 = 0.15$, $p = 0.002$, respectively).

Macroinvertebrate taxon richness did not differ

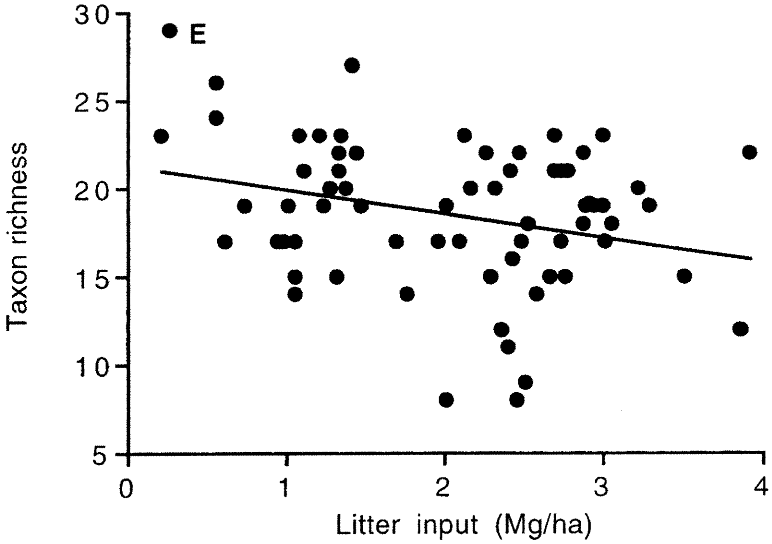

FIG. 3. Continued.

between the 2 watersheds, but did differ among landforms (ANOVA, $R^2 = 0.18$, $p < 0.006$), with higher richness in the outwash plain and end moraine than the ground moraine ($p < 0.05$). Non-Tanypodinae midges ($p = 0.009$), dytiscids ($p = 0.001$), and chaoborids ($p = 0.006$) each had higher relative abundance in Sucker Lakes ponds than in Rice River ponds. Dytiscid abundance varied significantly with landform ($R^2 = 0.33$, $p < 0.001$), with more beetles occurring in ponds in the outwash plain than in the ground and end moraines ($p < 0.05$). Pond basin size averaged 715.5 m^2 (SE = 56.4), ranging from 79 to 2141 m^2. Neither taxon richness ($p = 0.169$, Fig. 3C) nor relative abundance of any of the 18 widespread macroinvertebrate taxa was related to pond basin size (all $p > 0.01$). However, some taxa were probably missed in large ponds, basin size did not always reflect wetted area, and large habitats would support the most total invertebrates if abundances per sample were similar. Therefore, the lack of significant relationships between macroinvertebrate measures and basin size should be interpreted with caution.

TABLE 2. Water chemistry variables of 66 seasonal woodland ponds in northern Minnesota.

Variable	Mean (SE)	Range
pH	6.50 (0.05)	5.57–7.60
Alkalinity (μeq/L)	641.6 (78.8)	72–4347
Conductivity (μS/cm)	82.6 (7.1)	24–390
Color (absorbance units)	250.8 (8.2)	60–410
Total C (mg/L)	36.3 (1.1)	11.8–63.9
NH_4-N (mg/L)	0.56 (0.07)	0.06–3.03
NO_3-N (mg/L)	0.14 (0.02)	0.01–0.80
Total N (mg/L)	1.28 (0.07)	0.45–3.44
Total P (mg/L)	0.49 (0.05)	0.08–2.82

Canopy cover averaged 79.5% (SE = 2.6), with a median cover of 88%. Eight of 66 ponds were mostly open (<50% cover). Overstory tree basal area averaged 10.3 m^2/ha (SE = 1.3). The input of litter from trees averaged 2.03 Mg dry mass ha^{-1} y^{-1}, consisting of material from pond trees and shrubs and surrounding upland trees. Canopy cover, tree basal area, and litter input all were positively related ($p < 0.05$). Cover of CWD in ponds averaged 8.7% (SE = 0.8). Sedge (*Carex* spp.) was the most common herbaceous plant in ponds, averaging 56.3% cover (SE = 3.5, range 0–100%). Macroinvertebrate taxon richness increased with decreasing canopy cover ($r^2 = 0.16$, $p = 0.001$, Fig. 3D) and decreased with increasing litter input ($r^2 = 0.08$, $p = 0.021$, Fig. 3E). Numbers of dytiscids ($r^2 = 0.12$, $p = 0.005$), haliplids ($r^2 = 0.12$, $p = 0.004$), and hydrophilids ($r^2 = 0.14$, $p = 0.002$) were negatively related to canopy cover. Haliplid ($r^2 = 0.13$, $p = 0.003$) and dytiscid ($r^2 = 0.10$, $p = 0.012$) relative abundances were also negatively related to litter input. Hydrophilid relative abundance decreased

TABLE 3. Summary of canonical correspondence analysis (CCA) results, relating relative abundances of 18 widespread macroinvertebrate taxa to environmental variables in 66 seasonal woodland ponds in northern Minnesota. Overall CCA was significant at $p = 0.01$; CCA axis 1, $p = 0.155$ (Monte Carlo test).

	CCA axis			
	1	2	3	4
Eigenvalue	0.297	0.173	0.112	0.101
Taxa–environment correlation	0.727	0.821	0.731	0.737
Cumulative % variance of taxa	16.1	25.5	31.6	37.1
Cumulative % variance of taxa–environment relationship	33.8	53.4	66.1	77.6

($r^2 = 0.12$, $p = 0.004$), whereas limnephilid abundance increased ($r^2 = 0.10$, $p = 0.012$) with increasing CWD.

Multivariate analysis.—The first 4 axes of the CCA explained 37.1% of total variation ($p = 0.01$, Table 3) in relative abundances of the 18 widespread taxa; the first 2 CCA axes alone accounted for 25.5% of total variation (Fig. 4, Table 3). Axis 1 (16.1% of variation) was largely defined by tree basal area, pond hydroperiod, and occurrence of ponds in the glacial lake plain. Culicids and hydrophilids were associated with axis 1, being more abundant in ponds with low tree basal area and shorter hydroperiods; culicids were also less abundant in glacial lake plain ponds (Fig. 4). The Monte Carlo p-value of 0.155 for axis 1 indicates that, although this relationship explained the most variation, it was not strong. Axis 2 (9.4% of total variation) was defined by NH_4-N, total N, alkalinity, water color, and the occurrence of ponds in the outwash plain. In particular, ostracods, lymnaeids, planorbids, and to a lesser degree dytiscids, were more abundant in ponds with higher concentrations of NH_4-N and total N, higher alkalinity, and lower color, and in outwash plain ponds. In contrast, dixids and physids were somewhat more abundant in ponds with lower NH_4-N, total N, alkalinity, and higher color, and in ponds outside of the outwash plain. Axes 3 and 4 (6.1% and 5.5% of total variation, respectively, not shown in Fig. 4) were defined by conductivity and alkalinity (axis 3) and watershed (axis 4). Ponds having higher conductivity and alkalinity showed higher relative abundances of limnephilids, physids, planorbids, and tanypodines. Sucker Lakes ponds showed higher abundances of non-Tanypodinae midges, chaoborids, dytiscids, lumbriculids, and hydrophilids whereas Rice River ponds had higher abundances of lymnaeids and daphniids. Some associations identified by CCA were not detected in univariate analyses. For example, culicids were the macroinvertebrates most strongly associated with CCA axis 1, which accounted for most of the total variation. However, none of the univariate analyses between culicids and habitat characteristics were significant, probably because culicids were abundant in only 3 of 66 ponds. In addition to showing extremely high culicid abundances, those 3 ponds had low tree basal area and short hydroperiod. However, neither basal area nor hydroperiod explained significant variation in culicid abundance across all 66 ponds in the univariate analyses.

Relationships among macroinvertebrate taxa and between macroinvertebrates and amphibians

Relative abundances of dytiscids ($r^2 = 0.23$, $p < 0.001$), chaoborids ($r^2 = 0.23$, $p < 0.001$), and lumbriculids ($r^2 = 0.10$, $p = 0.012$) were positively related to relative abundances of non-Tanypodinae midges, and dytiscid and chaoborid relative abundances were positively related ($r^2 = 0.24$, $p < 0.001$). Planorbid, lymnaeid, and ostracod relative abundances were positively correlated (all $p < 0.001$). Ponds with larval wood frogs (ANOVA, $R^2 = 0.14$, $p = 0.002$) or blue-spotted salamanders ($R^2 = 0.08$, $p = 0.019$) each supported a greater number of macroinvertebrate taxa than ponds without these amphibians. Relative abundance of chaoborids was greater in ponds with frog larvae ($R^2 = 0.13$, $p = 0.003$) or salamanders ($R^2 = 0.12$, $p = 0.005$). Ponds with frog larvae ($p = 0.024$) or salamanders ($p = 0.006$) were wetter than ponds without amphibians.

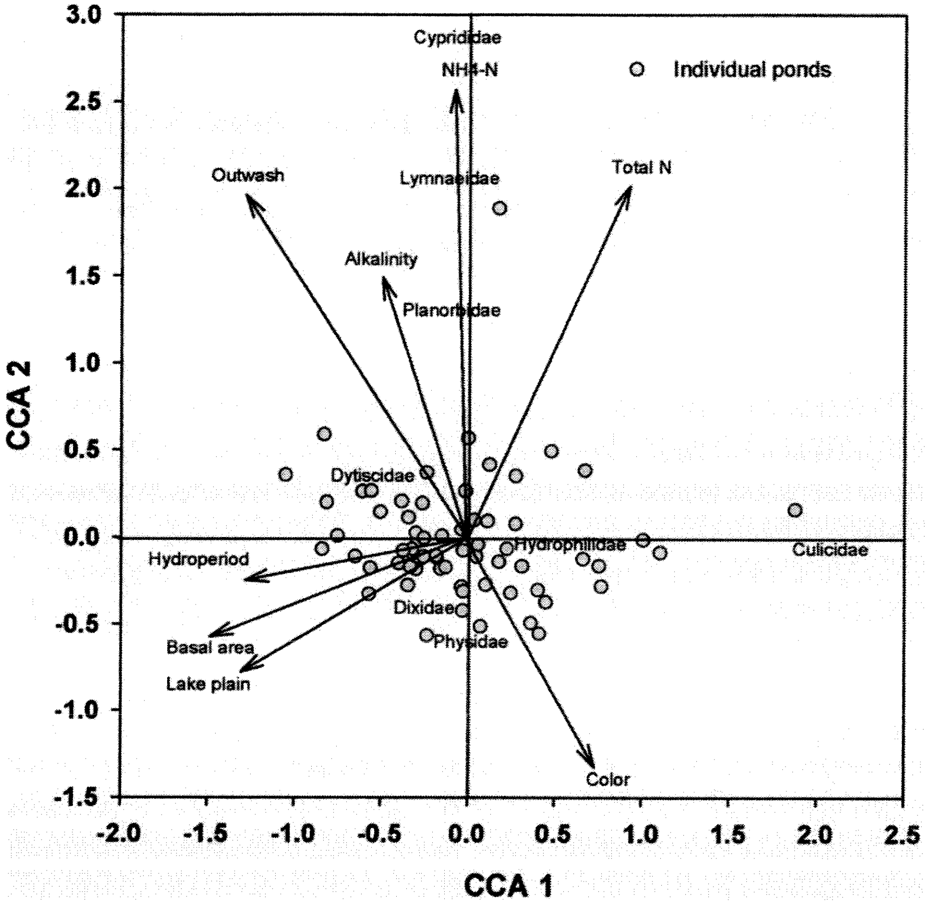

FIG. 4. Canonical correspondence analysis (CCA) ordination depicting relationships among relative abundances of widespread macroinvertebrates and environmental variables. The importance of an environmental variable in determining relative abundance of taxa in different ponds is reflected in the length and orientation of the arrows associated with each variable relative to the location of taxa and ponds on the triplot. For example, NH$_4$-N concentration is positively associated with ponds in the upper half of the triplot. These ponds had higher abundances of Cyprididae, Lymnaeidae, and Planorbidae. For clarity, only taxa and environmental variables having high discriminating power for distinguishing among ponds are shown.

Discussion

Numerous significant univariate and multivariate relationships between macroinvertebrates and environmental variables were detected (Table 4), but the more striking feature of our study was that most relationships were nonsignificant. Furthermore, most of the significant relationships were weak, explaining only 4 to 20% of variation. Taken together, the general lack of significant and strong relationships among macroinvertebrates and habitat variables may be the most important finding of our study.

Several factors may have contributed to our equivocal results. The value of species or genus vs family classification recently has been debated for streams (Bailey et al. 2001, Lenat and Resh 2001) and, in wetlands, taxonomic resolution at the family level or higher may mask significant relationships (King and Richardson 2002). Relationships at the genus or species level might not have been detected by using the family or subfamily level in our analysis for diverse groups (i.e., Tanypodinae and non-Tanypodinae midges, Dytiscidae, Hydrophilidae). However, 11 of 18 widespread taxa in our study consisted almost exclusively of one genus (i.e., Sphaeri-

TABLE 4. Statistically significant regressions (denoted by X) between environmental variables or composite canonical correspondence analyses (CCA) environmental axes and relative abundances of widespread macroinvertebrate taxa (ordered by highest to lowest % occurrence) and macroinvertebrate taxon richness from 66 seasonal woodland ponds in northern Minnesota. For simplicity, some univariate variables were grouped into more general categories, but macroinvertebrates may have only responded to a subset of variables in the category (i.e., geology–watershed, landform, pond size; ions–pH, conductivity, alkalinity; nutrients–NO_3-N, NH_4-N, total N, total P; dissolved C–total organic C, color; detritus–litter input, coarse woody debris; plant cover–sedge cover, tree basal area; vertebrates–frogs, salamanders). The most influential variables for each CCA axis were as follows: CC axis 1–composite of tree basal area, hydroperiod, and ponds outside of the lake plain; CCA axis 2–composite of NH_4-N, total N, alkalinity, and water color; CCA axis 3–composite of conductivity and alkalinity; and CCA axis 4–watershed. Taxon richness was not included in the CCA.

Invertebrate taxon	Hydro-period	Geol-ogy	Ions	Nutri-ents	Dis-solved C	Can-opy	Detri-tus	Plant cover	Verte-brates	CCA axis			
										1	2	3	4
Non-Tanypodinae Chironomidae		X											X
Lumbriculidae													X
Sphaeriidae	X												
Dytiscidae		X				X	X				X		X
Physidae											X	X	
Chaoboridae		X							X				X
Daphniidae													X
Culicidae										X			
Limnephilidae	X		X				X					X	
Planorbidae			X	X							X	X	
Tanypodinae												X	
Haliplidae	X					X	X						
Libellulidae	X												
Hydrophilidae						X	X			X			X
Cyprididae											X		
Ceratopogonidae				X									
Dixidae											X		
Lymnaeidae				X							X		X
Taxon richness	X	X	X			X	X		X	–	–	–	–

idae, Physidae, Planorbidae, Lymnaeidae, Daphniidae, Libellulidae, Limnephilidae, Haliplidae, Culicidae, Chaoboridae, Dixidae; Appendix), yet these taxa were no more responsive to environmental variation than the taxonomically diverse taxa (Table 4).

Our selection of ponds was restricted to those occurring in mature 2nd-growth forest thereby eliminating many sources of environmental variation. If ponds were environmentally homogeneous, then so too might macroinvertebrate communities. However, environments and macroinvertebrates were heterogeneous among ponds. For example, pond hydroperiods ranged from ephemeral to almost permanent (Fig. 2B), water chemistry variables routinely varied by 1 or 2 orders of magnitude (Table 2), and tree canopy and sedge cover ranged from negligible to 100%. Macroinvertebrate relative abundance was equally variable among ponds, with standard deviations for taxa frequently exceeding means.

It is also possible that sampling methods could have influenced results. Sweep nets collect large samples, but many taxa were probably missed with this method, especially in large ponds. Samplers that use mesh also have inherent biases. Small organisms may have passed through the mesh while others may have been pushed out of the front of the sampler when mesh clogged (Batzer et al. 2001). Moreover, our 4-date sampling schedule may have missed certain taxa that developed before, between, or after our sampling. These sources of error could have influenced results of individual analyses, but it seems unlikely that the general pattern of few or weak relationships between macroinvertebrates and habitat variables could have been eliminated simply by sampling refinements.

Statistical issues also could have influenced interpretation of results. Our sample size of 66 should have been sufficiently large to detect most patterns, which in fact likely contributed to detection of relationships that were statistically significant but explained only a minimal portion of variation. α-levels for individual tests are often reduced to account for repeated analyses, a practice questioned by Perneger (1998). If we had reduced α, even fewer of the univariate relationships detected in our study would have remained significant, thus exacerbating the pattern of nonconcordance between macroinvertebrate and environmental variables. The CCA was less fraught with such assumptions than univariate analyses but, like univariate tests, CCA accounted for only a few taxa and a minor amount of the total macroinvertebrate variation (37%). In summary, we acknowledge that the above factors influenced our results, but argue below that weak relationships between pond macroinvertebrates and their physical environment should be expected.

Weak influence of environmental variation on macroinvertebrates

Variation in hydroperiod was one of the stronger influences on macroinvertebrates in the seasonal woodland ponds (Table 4), but with some caveats. A relatively strong relationship between taxon richness and hydroperiod was detected; however, this association occurred primarily because rare taxa persisted only in the wettest ponds. In contrast, hydroperiod had relatively little influence on widespread taxa, in that the same macroinvertebrate taxa were numerically dominant whether ponds held water continuously or were dry for several months. Thus, it appears most organisms became abundant in ponds irrespective of hydroperiod, probably because the degree of variation in hydroperiod was insufficient to produce marked changes in widespread macroinvertebrate populations. Hydroperiod naturally varies unpredictably in many seasonal ponds, so macroinvertebrates that successfully exploit these habitats probably can tolerate a broad range of hydroperiod lengths. Hydroperiod probably restricts distributions of organisms that use seasonal woodland ponds as marginal habitats (i.e., rare taxa), but it may be relatively unimportant to successful taxa.

Our opinion on the importance of hydroperiod appears to contradict that of other studies in seasonal wetlands. Schneider and Frost (1996) in Wisconsin, Euliss et al. (1999) in North Dakota, Brooks (2000) in Massachusetts, and Fairchild et al. (2003) in Pennsylvania have all touted the importance of hydroperiod variation to invertebrates. However, those studies addressed extreme contrasts in hydroperiod. For example, of the 7 ponds studied by Schneider and Frost (1996), 1 was essentially permanent, whereas 2 others flooded for only 1 to 3 wk per year. Extremes in weather also affect hydroperiods and invertebrates in seasonal ponds. Euliss et al.

(1999) and Schneider (1999) both discussed how drought could induce major shifts in wetland invertebrate communities, and Golladay et al. (1997) reported that unusually wet conditions could do the same. Gross differences in hydroperiod should remain a defining feature to macroinvertebrates, which can explain faunal differences among varying classes of aquatic and wetland habitat (Wellborn et al. 1996). However, despite high variation in hydroperiod among our study ponds, it was probably still insufficient to influence most resident invertebrates.

Variation in water chemistry, surprisingly, did not affect macroinvertebrate taxon richness, and it influenced relative abundance of only a few of the 18 widespread taxa (Table 4). As with hydroperiod, water chemistry extremes among wetland ponds can affect macroinvertebrate distributions (Euliss et al. 1999). However, variation in chemical conditions among our study ponds, despite differences as great as 2 orders of magnitude, appeared insufficient to influence most macroinvertebrates. We suspect that most resident macroinvertebrates of Minnesota seasonal woodland ponds are capable of tolerating the natural range of water chemistry variation.

Pond hydrology and chemistry may vary annually. However, the geology and basin morphology (size) of ponds remains essentially constant. Thus, natural and consistent differences in geomorphology, as indicated by glacial landform and pond size, might exert significant influences on macroinvertebrate communities. However, only a few (and weak) relationships were detected between pond size and macroinvertebrates, and our prediction was not supported (but see caveats in Results section). Although relative abundances of some macroinvertebrates differed between the 2 watersheds and dytiscid relative abundance varied among landforms, mechanisms for these differences elude us. Perhaps the greatest influence of landform was that the density of ponds was highest in the ground moraine, with this landform thus providing more habitat for macroinvertebrates.

Like geomorphology, influences of vegetative characteristics on macroinvertebrates should remain consistent from year to year. Several associations were detected between macroinvertebrates and trees (canopy cover, basal area, litter input, CWD). However, the ecological significance of these relationships was not obvious. Detritivores (mollusks, non-Tanypodinae midges, limnephilids) that would be expected to respond to litter supplies were not associated with variables related to forest condition, whereas certain predators (dytiscids, hydrophilids), despite lacking a direct relationship, were influenced by these variables. Particularly perplexing were negative relationships between litter input and macroinvertebrate taxon richness and the relative abundances of some taxa. Leaf detritus was the most abundant food resource in ponds. Macroinvertebrate abundance and diversity in streams decline as leaf litter resources become limiting (Richardson 1991, Wallace et al. 1997). In seasonal woodland ponds, however, litter may be so abundant that macroinvertebrate detritivores rarely become food limited. Perhaps the negative relationship observed between macroinvertebrate richness and litter input was related to some harmful aspect of high litter abundance, such as increased biological oxygen demand (Battle and Golladay 2001).

Cause of variation in macroinvertebrates in seasonal woodland ponds

Wetland ecologists have been impressed with the highly variable nature of hydroperiods, water chemistries, and other habitat characteristics in seasonal ponds, and they often have assumed that such variation controls the equally variable macroinvertebrate communities. However, even with an extensive data set including a large number of seasonal woodland ponds and many habitat measures, we were able to explain only a small portion of the natural variation in macroinvertebrate richness and abundance among ponds. Numerous studies in wetlands have failed to find compelling relationships between invertebrates and the physical environment (Battle and Golladay 2001, Tangen et al. 2003, see reviews in Batzer and Wissinger 1996 and Batzer et al. 1999), yet few authors acknowledge that weak relationships are to be expected. Wetland invertebrates probably must endure high habitat variation frequently and thus have become tolerant to it; environmental variation may therefore not negatively affect many taxa in seasonal ponds (Williams 1996).

Existing hypotheses seem useful only for explaining gross patterns in macroinvertebrate community structure among seasonal ponds, elucidating differences between seasonal ponds and other kinds of habitat, or explaining why certain taxa do poorly in seasonal ponds. Such hypotheses are less suitable for explaining the ecology of macroinvertebrates in individual ponds or in complexes of seasonal ponds lacking extreme variation, or for interpreting the natural variation of common organisms. Most successful macroinvertebrates in ponds may be habitat generalists (Danks and Rosenberg 1987, Euliss et al. 1999, Tangen 2003), and thus their variation among or within ponds might be largely stochastic. Alternatively, distinct patterns in richness and relative abundance of macroinvertebrates might exist, but may be driven by unstudied factors. For example, patterns of colonization, especially those of flying insects, might be as important an influence on assemblage structure as interactions within an individual pond (Batzer 1995). In our study, most of the explainable variation occurred for aquatic insects, which because of flight can choose ponds to colonize. Flightless forms (mollusks, annelids, crustaceans) must endure whatever conditions develop, and they probably have evolved a durability that makes them little affected by habitat variation. We may need to explore new research directions, rather than continue using the tactic of simply defining fundamental niche constraints, to understand the ecology of macroinvertebrates in seasonal ponds.

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APPENDIX. Macroinvertebrates collected from 66 seasonal woodland ponds in northern Minnesota. Sampling was conducted in mid May and late June, 1998 and 1999. Individual samples consisted of pooled contents of three 1 m D-frame net sweeps. Numbers represent relative abundance (±1 SE) per pond sample. Relative abundances are presented only for higher taxa (e.g., families, subfamilies), but the most commonly collected genera for most groups are listed in order of relative abundance. Asterisks indicate that a macroinvertebrate was encountered on that date, but <0.1 organism per sample was collected. No entry = not collected.

	11–22 May 1998	17–25 June 1998	11–18 May 1999	16–23 June 1999
Platyhelminthes				
Tricladida	0.8 (0.3)	0.6 (0.6)	0.6 (0.3)	
Nematoda			1.0 (1.0)	
Mollusca				
Gastropoda				
Lymnaeidae	4.0 (1.4)	2.3 (0.7)	3.7 (1.1)	7.1 (1.8)
Stagnicola				
Physidae	19.4 (5.2)	18.7 (3.2)	6.4 (1.5)	27.3 (5.5)
Aplexa				
Physella				
Planorbidae	15.4 (5.6)	6.7 (2.3)	12.2 (2.7)	19.9 (7.3)
Gyraulus				
Promenetus				
Bivalvia				
Sphaeriidae	135.9 (27.2)	114.9 (15.5)	148.5 (18.7)	190.1 (23.9)
Sphaerium				
Annelida				
Oligochaeta				
Lumbriculidae	29.2 (9.9)	15.7 (3.9)	48.9 (17.4)	13.9 (3.1)
Lumbricidae			4.0 (1.7)	0.1 (0.1)
Hirudinea				
Erpobdellidae	1.3 (0.5)	1.2 (0.4)	0.5 (0.2)	1.1 (0.4)
Glossiphoniidae	0.4 (0.1)	1.4 (0.5)	0.8 (0.2)	1.1 (0.4)
Arthropoda				
Cladocera				
Daphniidae	28.7 (6.7)	5.0 (2.2)	57.6 (14.3)	10.5 (4.1)
Daphnia				
Anostraca				
Chirocephalidae	0.2 (0.2)		2.6 (1.0)	
Eubranchipus				
Conchostraca				
Lynceidae	2.5 (1.1)	2.4 (1.0)	46.1 (16.2)	30.6 (11.4)
Lynceus				
Notostraca				
Triopsidae	*	*	*	
Triops				

APPENDIX. Continued.

	11–22 May 1998	17–25 June 1998	11–18 May 1999	16–23 June 1999
Ostracoda				
Cyprididae	3.1 (1.4)	2.5 (1.9)	15.1 (5.4)	30.7 (21.1)
Acarina				
Hydrachnida	1.5 (0.4)	0.9 (0.4)	2.7 (0.6)	0.3 (0.1)
Ephemeroptera	*		*	
Odonata				
Coenagrionidae	0.1 (0.1)	0.9 (0.8)	*	
Nehalennia				
Lestidae	0.7 (0.2)	0.9 (0.4)	0.3 (0.2)	2.1 (0.4)
Lestes				
Libellulidae	1.3 (0.4)	2.5 (0.6)	0.4 (0.1)	2.2 (0.4)
Sympetrum				
Hemiptera				
Corixidae	0.5 (0.3)	2.4 (1.3)	0.2 (0.1)	4.5 (1.6)
Belostomatidae				*
Gerridae				0.3 (0.2)
Notonectidae	*	*		0.4 (0.3)
Notonecta				
Pleidae	*	*		*
Neoplea				
Trichoptera				
Hydroptilidae			*	
Leptoceridae	0.2 (0.2)	0.6 (0.6)	1.8 (1.8)	1.0 (1.0)
Oecetis				
Limnephilidae	17.7 (3.1)	1.5 (0.4)	5.9 (1.1)	1.3 (0.5)
Limnephilus				
Polycentropodidae	*	*	*	
Lepidoptera				
Pyralidae	*	*	0.3 (0.3)	*
Coleoptera				
Gyrinidae	0.5 (0.3)	0.6 (0.3)	0.3 (0.1)	0.2 (0.1)
Haliplidae	2.6 (0.9)	1.6 (0.4)	1.5 (0.3)	3.0 (0.6)
Haliplus				
Dytiscidae	2.3 (0.4)	2.4 (0.5)	1.9 (0.4)	4.3 (0.9)
Hydroporus				
Acilius				
Dytiscus				
Hydrophilidae	1.2 (0.3)	0.6 (0.1)	1.5 (0.3)	1.8 (0.6)
Berosus				
Tropisternus				
Scirtidae	0.1 (0.1)	0.1 (0.1)	0.1 (0.1)	0.2 (0.1)
Staphylinidae	*	*	0.1 (0.1)	*
Diptera				
Ceratopogonidae				
Forcipomyiinae	0.3 (0.3)	0.1 (0.1)	0.8 (0.6)	0.2 (0.2)
Ceratopogoninae	1.2 (0.5)	1.0 (0.4)	5.1 (2.3)	1.4 (0.6)
Chaoboridae	8.6 (2.3)	5.3 (2.6)	15.2 (2.2)	3.2 (0.8)
Mochlonyx				
Chaoborus				
Chironomidae				
Chironominae/ Orthocladinae	30.1 (9.0)	35.1 (8.8)	39.6 (7.7)	92.1 (17.2)
Chironomus				
Polypedilum				

APPENDIX. Continued.

	11–22 May 1998	17–25 June 1998	11–18 May 1999	16–23 June 1999
Tanypodinae	2.9 (1.1)	16.0 (9.4)	8.5 (2.3)	2.7 (0.9)
Larsia				
Psectrotanypus				
Culicidae	26.4 (21.1)	2.1 (1.2)	30.4 (14.1)	0.2 (0.1)
Aedes				
Culex				
Anopheles				
Dixidae	2.2 (0.6)	0.2 (0.1)	1.9 (0.6)	0.5 (0.2)
Dixella				
Tipulidae	*	*	0.3 (0.1)	*
Ephydridae	*		*	*
Stratiomyiidae	0.2 (0.2)	0.1 (0.1)	0.2 (0.1)	*
Syrphidae	*			*
Tabanidae	*	0.1 (0.1)	0.3 (0.1)	0.3 (0.2)