

Factors Affecting Distribution and Abundance of Aquatic Macroinvertebrates in
Autumnal Wetlands in Mammoth Cave National Park, Kentucky, U.S.A.

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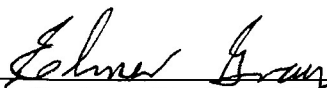
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Despite a recent surge of interest in temporary lentic systems, a strong theory linking the biota to its environment has not emerged. Data were collected from ten autumnal wetlands at Mammoth Cave National Park, Kentucky, U.S.A., in an effort to elucidate the environmental variables (EV's) that affected both between- and within-pond macroinvertebrate distribution and abundance. Canonical correspondence analyses performed with between-pond data failed to find strong relationships between the macroinvertebrates and EV's. Additionally, the theory that hydroperiod would effect richness did not apply to these ponds. Within-pond canonical correspondence analyses, however, yielded strong relationships. Further testing using regression analysis and Mann-Whitney U-tests demonstrated that macroinvertebrates were responding to a depth gradient. The presence of within-pond gradients, coupled with random dispersal, tolerant taxa, and ecological differences between vernal and autumnal wetlands, makes formulating a broad ecological theory difficult.

Introduction

Wetlands are generally defined as having hydric soils, water at or near the soil surface, a hydrophytic plant community, and a maximum water depth of 2 m (Cowardin et al., 1979). A temporarily inundated wetland has a fairly predictable hydrologic cycle and usually dries annually. Temporary wetlands have been historically overlooked because they were thought to be too small for waterfowl use and species poor. Past government policies encouraged the draining and filling of wetlands for agricultural use or development. Dahl (1990) estimated that from the 1780's to the 1980's 53% of the wetlands were lost in the conterminous United States. Since the mid-1980's, however, there has been a surge of interest in temporary wetlands mainly due to new laws protecting wetlands, the realization of their biodiversity, and growing knowledge of their intrinsic values.

Macroinvertebrates are one of the most important and diverse groups of organisms in temporary wetlands (Batzer et al., 1999). Complex communities exist in temporary wetlands, but a strong, holistic theory linking the distribution and abundance of taxa to the physical and biotic properties of temporary wetlands still eludes ecologists (Battle and Golladay, 2001; Tangen et al., 2003; Batzer et al., 2004; but see Schneider, 1999).

Coping with, or avoiding, desiccation is one of the most important life-history constraints for macroinvertebrates in temporary wetlands. Wiggins et al. (1980) divided inhabitants into four groups based on their strategy for coping with pond drying: (1) group one taxa are year-round residents, capable of passive dispersal only. They cope with pond drying in an egg, cyst, juvenile, or adult form; (2) group two taxa are overwintering spring recruits. Individuals must reproduce and oviposit before the pond

dries. They cope with pond drying as eggs or larvae, but rarely as adults; (3) group three taxa can oviposit without water and overwinter as eggs or larvae; and (4) group four taxa are non-wintering spring migrants. These individuals must oviposit in water, and the offspring must grow and leave the pond before it dries. Taxa must overwinter in permanent water.

Hydroperiod (the number of days that a pond holds water) and two related factors, pond area and habitat complexity, are commonly cited as the main factors controlling both richness and abundance (Wiggins et al., 1980; Schneider and Frost, 1996; Welborn et al., 1996; Euliss et al., 1999; Higgins and Merritt, 1999; Magee et al., 1999; Schneider, 1999; Wissinger et al., 1999; Brooks, 2000; Fairchild et al., 2003). Schneider (1999) showed that hydroperiod acted as a sieve, that is, the presence of taxa in ponds were additive as hydroperiod increased. Hydroperiod also affects predation and competition (Wilbur, 1997). Ponds with short hydroperiods are relatively predator- and competitor-free since initial colonizers are usually detritivores and there is a surplus of food and space (Wiggins et al., 1980). As hydroperiod increases, predation and competition become major factors in structuring communities (Wilbur, 1980; Higgins and Merritt, 1999). Additionally, long-duration ponds may be colonized by taxa that have no adaptations to cope with pond drying (Schneider and Frost, 1996).

While hydroperiod has been the most studied factor, pH (Haack et al., 1989; Gorham and Vodopich, 1992; Euliss et al., 1999), dissolved oxygen (Battle and Golladay, 2001), nutrient levels (Schalles and Shure, 1989; Gabor et al., 1994; Bonner et al., 1997), landform type (Batzer et al., 2004), and surrounding land use (Euliss and Mushet, 1999) have also been assumed to contribute to temporary pond macroinvertebrate assemblages.

Unfortunately, clear and concise relationships between invertebrate communities and environmental variables (EV's) have not emerged. Most research searching for relationships has found significance only along extreme environmental gradients (Batzer et al., 2004).

At temperate latitudes, temporary ponds can be classified as either vernal or autumnal (Wiggins et al., 1980). Vernal ponds fill in spring, usually from snowmelt, and dry in summer. Autumnal ponds fill in fall, persist through winter and spring, and also dry during summer. Most temporary wetland research has been performed on vernal ponds. Studies on autumnal ponds have been far more infrequent (e.g. Batzer and Sion, 1999; Wissinger et al., 1999). Wiggins et al. (1980) warned that the differences between the effects exerted by vernal and autumnal ponds should not be overlooked and likely influences macroinvertebrate communities. Most temporary pond theories and generalizations are based on vernal pond research, leaving autumnal ponds and their biota relatively unexplored.

Data concerning within-pond gradients are sparse. Brooks (2000) realized that a temporary pond contained concentric biotic zones. As a pond dries, habitat is lost from the more ephemeral outermost zone. Higgins and Merritt (1999) speculated that the size and duration of a pond during its wettest phase influenced macroinvertebrate communities. Fairchild et al. (2003) investigated microhabitat influences on aquatic beetle assemblages and found higher abundances near shore, possibly responding to increased temperature and dissolved oxygen.

The goal of my study was to determine if ten autumnal wetlands in Mammoth Cave National Park, Kentucky, U.S.A., adhered to current temporary wetland paradigms. I tried to answer the following series of questions:

1. Can the between-pond distribution and abundance of macroinvertebrates be related to pond EV's, and more specifically, what effect does hydroperiod have?
2. Does the within-pond distribution and abundance of macroinvertebrates respond to EV's?
3. Can generalizations regarding vernal ponds be applied to autumnal ponds?

Methods

Study Area

Research was performed on ten autumnal wetlands in Mammoth Cave National Park, Kentucky, USA. The ponds are classified as palustrine forested wetlands by the Cowardin classification system (Cowardin et al., 1979) and are located within the Crawford-Mammoth Cave Upland Level IV Ecoregion (Interior Plateau Level III Ecoregion; Woods et al., 2002). This region is characterized by sandstone cliffs and limestone valleys. All ten ponds have a similar land use history dating back to 1941 when this area was converted to a national park. The ponds are within 4 km of each other (Figure 1) and are 1.2 - 3.2 km from the nearest permanent body of water. This region receives an average of 132 cm of rain per year, with October (7.4 cm) and March (14.3 cm) being the driest and wettest months, respectively (World Climate, 2003a). This region experiences hot summers (average daily temperature in July is 24.4 °C) and cool winters (average daily temperature in January is 0.7 °C) (World Climate, 2003b). During

the study period all ponds filled in November and were dry by August, classifying the wetlands as autumnal ponds (Wiggins et al., 1980).

Some ponds have an overflow channel that limited their maximum size (e.g., pond 6, Figure 2). Additional water was directed through the overflow channel and down an adjacent ridge. There were no surface water connections between ponds, and there were no connections to permanent water bodies. Pond 1 was the only unit that had a surface inlet, which was similarly temporary.

The ponds are surrounded by a second growth mixed hardwood forest, consisting mainly of white oak (*Quercus alba*), northern red oak (*Q. rubra*), scarlet oak (*Q. coccinea*), blackgum (*Nyssa sylvatica*), red maple (*Acer rubrum*), yellow poplar (*Liriodendron tulipifera*), beech (*Fagus grandifolia*), and redcedar (*Juniperus virginiana*). The canopy is moderately dense with a thin underbrush consisting of *A. rubrum* and raspberry (*Rubus* spp.).

Environmental variables

Perpendicular transects that radiated in cardinal directions from the deepest point of each pond were marked in November 2003. Specific conductivity, pH, and dissolved oxygen were taken along these transects at each invertebrate sampling point (n = 20 per pond) with a Hydrolab Series 4a multiprobe sonde. HOBO Water Temp Pro data loggers were placed at the deep point of each pond in January and retrieved in July after each pond had dried. The data loggers collected data hourly, from which I was able to calculate mean temperature and variance. Hydroperiod length was determined from the temperature graphs. As the ponds dried, the data loggers were no longer buffered by

water and obvious temperature spikes were observed. Water samples for laboratory analysis of ammonia-nitrogen, nitrate-nitrogen, ortho-phosphates, and total phosphorus were obtained in December 2003 and March 2004, and analyzed by the Western Kentucky University Ogden Environmental Water Quality Laboratory according to standard methods (AHPA, 1998).

Pond mapping was performed in June 2004, when the high water marks were clearly visible and pond vegetation was at its maximum. The maps in Figure 2 were created using a tape measure, compass, and laser range finder. Area and vegetation were calculated by using scaled jpg. images and an overlying grid (Microsoft Photodraw, Version 2.0 for Windows, Microsoft Corporation, 2000). Volume was calculated by multiplying the mean depth and area.

Following complete desiccation of all ponds, coarse woody debris (CWD) and fine woody debris (FWD) were quantified. Length and diameter of all CWD (3+ cm diameter) and FWD (1-2 cm diameter) within 0.5 m of the predetermined transects were measured (Harmon et al., 1986). Woody debris values were divided by the transect area to achieve a measure of debris density.

Macroinvertebrates

Pond macroinvertebrates were sampled using two methods. First, the ponds were sampled with a benthic core sampler (0.005 m²) in winter (31 January - 1 February 2004) and spring (3 - 4 April 2004). During each sampling event, ten core samples per pond were taken along the predetermined transects at set distance proportions (2%, 10%, 20%, 30%, 40%, 50%, 60%, 70%, 80%, and 100%) from the pond margin to the deepest point.

This procedure allowed for even sampling of the range of depths present (assuming a bowl-shaped pond) and attempted to counter the tendency to over-sample deeper areas. The benthic corer was pushed into the substrate until it reached an impermeable clay layer (usually 4-8 cm). Each sample was rinsed through a 500 μm sieve and preserved in 95% ethyl alcohol.

Ponds were also sampled in spring (17 - 18 April 2004) with a sweep net (500 μm). The net was pulled laterally through the water column using three one-meter sweeps, with the last one scraping the bottom. The ponds were sampled at the margin, the deepest point, and once midway between the edge and deepest point or in a habitat type previously underrepresented (Batzer et al. 2004). The three samples were combined for each pond and processed in identical fashion to the cores.

In the laboratory, samples were again rinsed through a 500- μm sieve and sorted under dissecting microscopes. Identification was performed using Thorp and Covitch (1991), Merritt and Cummins (1996), and Epler (2001). Taxa were assigned to life history (Wiggins et al., 1980), functional feeding (Thorp and Covitch, 1991; Merritt and Cummins, 1996; Barbour et al., 1999), and respiration groups (Thorp and Covitch, 1991). In addition, both taxa richness and evenness were calculated. The evenness value represents the proportion of individuals that belonged to the five most abundant taxa in each pond.

Statistical analysis

Some macroinvertebrate taxa were removed prior to all analyses. Collembola are semiaquatic, and nematodes are not properly retained in 500 μm sieve or sweep net. A

single *Acroneuria sp.* (Plecoptera, Perlidae) was removed, its having been in the pond with the shortest hydroperiod. Additionally, parasites, such as mites, were removed.

Statistical analyses were broken into two steps. The first investigated EV's that may have contributed to differences in aquatic macroinvertebrate assemblages between ponds. The second was a within-pond approach, which attempted to relate EV's collected at every sampling point with the invertebrate assemblages.

The between-pond analysis started with 38 EV's, which were subsequently reduced in number to meet assumptions of a canonical correspondence analysis (CCA; ter Braak, 1986). A CCA, which attempts to find relationships between two matrices using multiple linear regressions, is in danger of producing a type II error when the number of environmental variables approaches or exceeds the number of observations or samples (McCune and Grace, 2002). Redundant variables were first identified with a Pearson Correlation analysis and removed. CCA's with forward selection were then employed to further reduce the EV's from eight to five.

The between-pond CCA's were performed with EV's and five biotic matrices: winter cores, spring cores, means of both cores, sweep data, and presence/absence using all samples. Due to the different sampling methods, core samples were pooled with the sweep net samples to make a binary matrix. The cores collected in the winter were initially kept separate from the spring cores but were eventually averaged to obtain a larger data set. I assumed the metrics would respond linearly to the EV's (van den Wollenberg, 1977) and used a redundancy analysis (RDA). A series of linear regressions relating abundance and richness to the EV's was used to support the results of both the CCA's and RDA and to test the hydroperiod hypotheses.

CCA's were then used to relate within-pond EV's to the macroinvertebrate assemblages for each of the two core sampling events. Since only depth, pH, DO, temperature, and distance from margin were measured at each sampling point, reduction of the EV's was not necessary. The within-pond temperature data for the spring cores needed to be standardized due to the time of day they were collected. As the sampling progressed through the day, the ponds warmed, making temperature comparisons unrealistic. I adjusted the shallowest sample to 10°C, and then adjusted the rest of the temperatures of the pond the same amount as the first. This preserved their relationships and made them comparable. The winter cores did not require standardization due to the presence of surface ice throughout the sampling period. A series of linear regressions relating abundance and richness to the EV's was also used to support the results of the CCA's.

Mann-Whitney U-tests were used to test for differences in mean abundance and richness of the core samples placed into two depth groups. Using a natural break in the sample depth frequency, samples from 0.01 m to 0.38 m were classified as shallow cores and samples from 0.40 m to 0.90 m were classified as deep cores. Core samples were also grouped by their distance from the pond margin. Again, using a natural break, all samples less than 3.0 m from the margin were designated as near-margin samples, and samples at 3.5 m and greater were designated as central samples. Additionally, abundance and richness were compared within the created distance zones. The near-margin samples from shallow ponds (no samples over 0.38 m) were compared to near-margin samples from deep ponds (some samples over 0.39 m), and central core samples from shallow ponds were compared to central core samples from deep ponds.

All Monte Carlo tests used 999 iterations. For both sets of CCA's, metrics and environmental variables except pH were either $\ln(x+1)$ -transformed or $\arcsin(x^{1/2})$ -transformed. Invertebrate abundance data was also $\ln(x+1)$ -transformed. CANOCO (Version 4.5 for Windows, Agricultural Mathematics Group, Wageningen, The Netherlands) was used for all CCA's and the RDA. SPSS (Version 12.0 for Windows, SPSS inc., 2003) was used for Pearson Correlation analyses, linear regressions, and Mann-Whitney U-tests.

Results

Environmental variables

The ponds varied along several physical and biotic variables (Table 1, Table 2). Mean depth ranged from 0.04 - 0.59 m and was correlated with hydroperiod ($p = 0.001$), which ranged only from 218 - 284 days. The ponds varied in area from 193 - 1025 m², and volume ranged from 12 - 285 m³. Area was not correlated with depth ($p = 0.313$) or hydroperiod ($p = 0.567$).

DO means ranged from 1.4 to 9.8 mg/L. Levels were typically higher in the spring (compared to the winter) when macrophytic coverage was higher. There was a spatial gradient of DO in ponds that had macrophytes. DO readings were typically higher when taken in or near aquatic vegetation, and tended to be low at the deepest areas of the ponds. DO was significantly correlated with aquatic macrophytic coverage ($r^2 = 0.41$, $p = 0.045$). All ponds were acidic with mean pH values ranging from 4.8 - 6.4.

Habitat complexity was variable among the ponds. Aquatic macrophytic coverage ranged from 0 to 100%, with most ponds having less than 10%. Pond 12 was the sole

unit that was covered completely with aquatic macrophytes, and was also the only pond with duckweed (*Lemna* sp.). Surface areas of CWD and FWD per m² were combined to best represent habitat complexity with a single woody debris variable. Woody debris ranged from 0.04 – 0.33 m²/m² and was not correlated with pond area ($p = 0.521$). Chemical data (ammonia-nitrogen, nitrate-nitrogen, ortho-phosphates, and total phosphorus) were removed due to the high variability between the winter and spring data.

Macroinvertebrates

A total of 18,585 macroinvertebrates belonging to 35 taxa (Appendix A) were collected. Taxa were added with each new sampling period, and the sweep net data yielded the most taxa (Table 3). Isopoda, Copepoda, Ostracoda, and Oligochaeta were the only taxa to occur in all ten ponds (Appendix A). Significantly more macroinvertebrates were collected in the spring cores versus the winter cores (u -value = 0.020, $n = 200$).

Richness ranged from 10 to 21 taxa per pond (Table 4). Most taxa gathered oxygen via gills or cutaneous respiration. Atmospheric air breathers (mostly dytiscids) were not common. Most taxa were categorized as overwintering residents (groups 1-3) and filtering-collectors or gathering-collectors due to the dominance of isopods and copepods.

Between-pond relationships between macroinvertebrates and pond variables

Only one CCA or RDA was able to find significant relationships between the macroinvertebrate matrices and the pond EV's (Table 5). The sweep net data yielded a CCA that was significant on the first axis ($p = 0.006$) and all four axes ($p = 0.028$). The

only significant regression was a positive relationship between area and richness (Table 6). Hydroperiod was not significantly related to richness ($r^2 = 0.03$, $p = 0.654$).

Within-pond relationships between macroinvertebrates and pond variables

The CCA results were significant for both the winter and spring data (Table 7, Figures 3 and 4). Regressions showed a consistent relationship between depth and both abundance and richness (Table 8). Abundance and richness were significantly higher ($u < 0.001$, $u = 0.002$) in the shallower samples (Figure 5). Mean abundance and richness was then compared between 2 groups based on the relative distance from the pond margin (near shore, $n = 100$, central, $n = 100$). Abundance ($u = 0.012$), but not richness ($u = 0.285$), was higher in the samples taken from the near-margin area of each pond (Figure 5). The near-shore samples from shallow ponds did not significantly differ from near shore samples from deep ponds in richness ($u = 0.944$). Central core samples from shallow and deep ponds did not significantly differ in abundance ($u = 0.060$) or richness ($u = 0.326$; Figure 5).

Discussion

The lack of clear relationships from the between-pond analyses share similarities with recent research (Wissinger, 1999; Batzer and Sion, 1999; Batzer et al., 2004). There may be a new theory emerging claiming that weak relationships between macroinvertebrates and EV's should be expected (Wissinger, 1999; Batzer et al., 2004). Most macroinvertebrates existing in temporary wetlands are generalists, coping with desiccation, low DO, and warm temperatures. If considerable within-pond variation

exists, it may be unrealistic to assume that macroinvertebrate communities will respond to differences between ponds.

Macroinvertebrate richness was not significantly related to hydroperiod. The significant regression between richness and area may be explained by the effect of the size of an island in island biogeography, an ecological theory that predicts a higher probability of colonization with a larger pond (MacArthur and Wilson, 1967). That area was not correlated with depth or hydroperiod supports this theory. Other studies have yielded mixed conclusions about the effects of area (Pearman, 1995; Brose, 2003; Batzer et al., 2004), which is usually related to canopy cover, hydroperiod, and habitat complexity.

I believe that the lack of between-pond relationships is not spurious, but there are some important considerations. The lack of a clear relationship may be due to the low number of sampling events, the low variance in hydroperiod, or statistical noise. Richness in the ten ponds was lower than other studies, but was most likely due to the use of a benthic core sampler and having only one combined sweep net sampling event. Batzer et al. (2004), in a large 66-pond study in northern Minnesota, also contradicted the effects of hydroperiod on richness. They found a positive relationship between richness and hydroperiod, but partially dismissed this relationship because of the many rare taxa that were found in the wettest ponds.

Variance in hydroperiod was lower than other studies (Schneider, 1999; Wissinger et al., 1999; Brooks, 2000; Batzer et al., 2004) and lower than what may be expected from such a wide range in area, depth, and volume. This may be inherent to the fact that autumnal ponds tend to be deeper than vernal ponds (Higgins and Merritt 1999,

Wissinger et al. 1999). Autumnal ponds persist until the heat of mid-summer, when evaporation rates are at their highest and dry rapidly.

Finally, the few significant CCA's may be due, in part, to natural statistical noise present in the macroinvertebrate data. For example, 553 of the 554 *Culex* sp. were collected from one pond. In addition, all 155 *Sphaerium occidentale* were sampled from one pond. To say that these distributions are random is presumptuous, but assuming they are relevant may also be dangerous. Random dispersal of taxa coupled with non-dispersing group one taxa makes dealing with absolute rarity or pond-occurrence rarity difficult. Brose (2003) concluded that in a cluster of ponds, good dispersers could counteract local environmental effects. Batzer and Sion (1999) stated that random colonization events strongly shaped the communities in their autumnal ponds. Fearing the loss of information and to avoid misrepresenting the ponds, rare taxa were not removed from the analyses.

Within-pond analyses indicated that macroinvertebrates responded to a depth gradient (Table 8). My research also showed significant differences between abundance and richness in deep and shallow areas of the ponds. Fairchild et al. (2003) found similar results with beetle assemblages. The shallow margins of a pond provide many benefits. Dissolved oxygen and temperature may be higher, allowing for faster development (Fairchild et al., 2003). Higgins and Merritt (1999) suggested that the pond margins, being the last to be inundated, might have the most conditioned detritus. They explained that terrestrial fungi, bacteria, and protozoa colonize dry detritus, which, when it becomes inundated, feeds a fast-growing microbial community that supports a thriving gathering-

collector assemblage. Gatherer-collectors were the dominant functional feeding group in most ponds (Table 4).

My data did not show a DO response to depth, possibly due to rooted aquatic macrophytes being absent in very shallow waters or the use of an imprecise DO sensor. The significant relationship between macroinvertebrate abundance and temperature was due to the correlation between temperature and depth: A positive relationship existed in the winter and a negative relationship in spring (Table 8). Macroinvertebrates utilized the pond margin throughout inundation regardless of temperature.

Developing a holistic theory relating macroinvertebrate communities to EV's may be difficult due to the unwarranted combining of vernal and autumnal ponds. Autumnal ponds, due to their longer hydroperiods, can contain taxa that do not have specific adaptations to cope with pond drying. Batzer and Sion (1999) stated that pond drying might be less disruptive in autumnal ponds than vernal ponds. It is possible that the lesser severity of the shorter dry season does not effectively limit some taxa that would otherwise be eliminated by pond drying. Isopods, which are rare in temporary ponds with no permanent water connection (Wiggins et al. 1980), existed and thrived in the shortest hydroperiod pond. Another example, *Chauliodes* sp. (Megaloptera, Corydalidae), which was observed in autumnal pools by Batzer and Sion (1999), is thought to have no desiccation resistance. Three *Chauliodes* sp. were collected from a pond with a 240-day hydroperiod and a soft muck bottom. *Chauliodes* sp. may avoid the shortened dry season of an autumnal pond by burrowing into the mud. The increased presence of unadapted taxa in autumnal ponds, in relation to vernal ponds, undoubtedly affects predation, competition, and ultimately the macroinvertebrate communities.

Autumnal pond macroinvertebrates are generalists that may or may not have known adaptations to cope with, or avoid, pond drying. Their dispersal can be random, and once in a pond, they will seek out the best habitat. I conclude that these characteristics make between-pond analyses difficult, especially if the ponds are not drastically different. Within-pond analysis, however, seems more promising in describing and predicting macroinvertebrate assemblages. Future research using a balanced within-pond sampling effort, larger sample sizes, and the creation of multiple concentric zones within a pond could give insight to the within-pond distribution phenomenon.

Table 1. The eight EV's from which the final five were selected for use in the between-pond CCA's comparing the macroinvertebrate assemblages to the EV's. * indicates the five EV's used in the CCA's.

Pond	hydroperiod		area * (m ²)	temperature (°C) *			DO (mg/L) *		
	N	range		mean +/- SD	N	range	mean +/- SD		
1	218		805	3647	4.0-25.2	12.9 +/- 5.7	20	1.2-12.8	8.0 +/- 3.0
2	247		1025	3815	0.8-24.1	12.6 +/- 6.3	19	0.6-11.4	5.8 +/- 4.0
3	284		193	4535	5.2-20.9	12.0 +/- 4.5	20	1.1-4.8	2.5 +/- 1.2
5	261		673	3983	4.0-21.9	11.3 +/- 5.3	18	1.4-8.1	3.9 +/- 2.0
6	247		445	3825	4.5-25.9	13.5 +/- 6.0	20	1.0-11.1	4.8 +/- 3.4
7	254		798	3837	4.7-22.9	12.5 +/- 5.6	20	0.6-12.2	5.0 +/- 3.3
9	272		630	4262	4.1-25.7	13.5 +/- 6.3	20	1.1-6.4	3.7 +/- 2.2
10	218		350	3655	0.0-34.3	13.1 +/- 8.0	14	0.5-3.7	1.7 +/- 1.2
11	254		248	3833	4.2-24.6	12.7 +/- 6.0	20	0.8-2.3	1.4 +/- 0.4
12	240		253	3647	2.9-24.1	12.4 +/- 6.0	20	0.7-18.6	9.8 +/- 4.0

Pond	depth (m) *			pH *			macrophyte coverage	woody debris (m ² /m ²)
	N	range	mean +/- SD	N	range	mean +/- SD		
1	20	0.05-0.26	0.14 +/- 0.06	20	4.8-6.0	5.1 +/- 0.3	6%	0.15
2	20	0.03-0.25	0.14 +/- 0.06	20	4.6-6.1	5.5 +/- 0.4	69%	0.14
3	20	0.10-0.89	0.59 +/- 0.26	20	5.6-5.9	5.8 +/- 0.1	4%	0.33
5	20	0.06-0.90	0.42 +/- 0.27	20	4.1-5.4	4.8 +/- 0.5	3%	0.18
6	20	0.05-0.34	0.19 +/- 0.09	20	4.1-5.5	4.9 +/- 0.5	8%	0.12
7	20	0.03-0.45	0.22 +/- 0.13	20	4.2-5.5	4.8 +/- 0.5	66%	0.21
9	20	0.04-0.69	0.34 +/- 0.20	20	4.1-7.3	5.0 +/- 0.8	1%	0.08
10	20	0.01-0.09	0.04 +/- 0.03	14	6.1-6.7	6.4 +/- 0.2	7%	0.14
11	20	0.03-0.58	0.37 +/- 0.17	20	4.4-6.0	4.9 +/- 0.4	<1%	0.26
12	20	0.02-0.27	0.16 +/- 0.06	20	4.9-5.8	5.5 +/- 0.2	100%	0.04

Table 2. EV's used in the within-pond CCA's relating the macroinvertebrate assemblages to the EV's.

Pond	DO (mg/L)		depth (m)	
	N	range	mean +/- SD	mean +/- SD
1	20	1.2-12.8	8.0 +/- 3.0	20 0.05-0.26 0.14 +/- 0.06
2	19	0.6-11.4	5.8 +/- 4.0	20 0.03-0.25 0.14 +/- 0.06
3	20	1.1-4.8	2.5 +/- 1.2	20 0.10-0.89 0.59 +/- 0.26
5	18	1.4-8.1	3.9 +/- 2.0	20 0.06-0.90 0.42 +/- 0.27
6	20	1.0-11.1	4.8 +/- 3.4	20 0.05-0.34 0.19 +/- 0.09
7	20	0.6-12.2	5.0 +/- 3.3	20 0.03-0.45 0.22 +/- 0.13
9	20	1.1-6.4	3.7 +/- 2.2	20 0.04-0.69 0.34 +/- 0.20
10	14	0.5-3.7	1.7 +/- 1.2	20 0.01-0.09 0.04 +/- 0.03
11	20	0.8-2.3	1.4 +/- 0.4	20 0.03-0.58 0.37 +/- 0.17
12	20	0.7-18.6	9.8 +/- 4.0	20 0.02-0.27 0.16 +/- 0.06

Pond	pH		temperature (°C)		distance		
	N	range	mean +/- SD	mean +/- SD	N	range	mean +/- SD
1	20	4.8-6.0	5.1 +/- 0.3	20 0-11.3 5.5 +/- 4.7	20	0.1-12.1	5.4 +/- 3.2
2	20	4.6-6.1	5.5 +/- 0.4	20 0-11.0 4.8 +/- 4.2	20	0.1-14.7	6.4 +/- 4.2
3	20	5.6-5.9	5.8 +/- 0.1	20 0-10.0 3.9 +/- 2.6	20	0.1-7.1	3.1 +/- 2.3
5	20	4.1-5.4	4.8 +/- 0.5	20 0-10.0 4.0 +/- 2.4	20	0.1-11.1	6.1 +/- 3.7
6	20	4.1-5.5	4.9 +/- 0.5	20 0-11.6 5.2 +/- 3.3	20	0.1-7.8	3.8 +/- 2.5
7	20	4.2-5.5	4.8 +/- 0.5	20 0-10.5 5.4 +/- 4.3	20	0.1-8.0	4.6 +/- 2.8
9	20	4.1-7.3	5.0 +/- 0.8	20 0-10.0 5.4 +/- 3.5	20	0.1-1.01	5.2 +/- 3.1
10	14	6.1-6.7	6.4 +/- 0.2	20 0-10.3 5.2 +/- 4.9	20	0.1-7.4	3.5 +/- 2.1
11	20	4.4-6.0	4.9 +/- 0.4	20 0-10.2 6.3 +/- 3.6	20	0.1-7.5	3.3 +/- 2.0
12	20	4.9-5.8	5.5 +/- 0.2	20 0-12.9 4.0 +/- 4.5	20	0.1-9.7	4.0 +/- 3.1

Table 3. Taxa sampled and new taxa found during each sampling event.

		Pond										
		1	2	3	5	6	7	9	10	11	12	
winter cores	# taxa sampled	11	6	3	8	10	8	10	5	8	4	
spring cores	# taxa sampled	8	10	7	10	10	7	11	8	8	8	
	# new taxa	0	4	4	4	1	0	3	4	1	5	
sweeps	# taxa sampled	15	17	10	12	13	19	16	8	7	16	
	# new taxa	7	7	3	6	5	13	5	4	1	8	
all samples	# taxa sampled	18	17	10	18	16	21	18	13	10	17	

Table 4. Various metrics used in the analysis. Functional feeding group data were combined from Barbour et al. (1999) and Merritt and Cummins (1996). GC = gatherer/collector, FC = filtering collector, PR = predator, SC = scraper, and SH = shredder. Oxygen acquisition data was taken from Thorp and Covitch (1991). AT = atmospheric, CU = cutaneous, and GL = tracheal gills. Life history classes are based on Wiggins et al. (1980).

	Pond richness	evenness, %	functional feeding group, %				
			FC	GC	PR	SC	SH
1	18	81	3	83	1	4	8
2	17	83	17	58	1	5	19
3	10	96	19	79	2	0	0
5	18	92	56	35	7	0	2
6	16	89	20	72	2	0	7
7	21	92	18	77	4	0	<1
9	18	91	30	65	5	0	<1
10	13	>99	9	91	<1	<1	<1
11	10	96	1	92	1	2	5
12	17	89	3	88	8	0	1

	Pond oxygen acquisition, %			life history class, %			
	AT	CU	GL	1	2	3	4
1	<1	87	12	30	69	0	<1
2	1	46	53	72	27	0	1
3	0	61	39	96	2	<1	2
5	4	76	21	88	7	<1	5
6	2	52	46	89	10	<1	1
7	2	41	57	93	3	1	3
9	<1	57	42	87	8	<1	5
10	9	1	90	91	<1	9	<1
11	1	19	80	95	5	0	0
12	5	93	2	87	10	<1	3

Table 5. Results of the between-pond CCA analyzing relationships between macroinvertebrate assemblages and pond EV's.

Winter cores					Total
Axes	1	2	3	4	inertia
Eigenvalues	0.34	0.19	0.16	0.10	1.63
Cumulative percent variance of species data explained	20.8	32.6	42.2	48.2	
Test of significance:					
Axis 1: $F = 1.05$, $p = 0.412$					
All canonical axes: $F = 0.92$, $p = 0.604$					

Spring cores					Total
Axes	1	2	3	4	inertia
Eigenvalues	0.22	0.16	0.12	0.09	1.01
Cumulative percent variance of species data explained	21.8	37.7	49.5	57.9	
Test of significance:					
Axis 1: $F = 1.12$, $p = 0.471$					
All canonical axes: $F = 1.30$, $p = 0.138$					

Mean cores					Total
Axes	1	2	3	4	inertia
Eigenvalues	0.22	0.15	0.13	0.08	1.04
Cumulative percent variance of species data explained	21.0	35.2	47.8	55.0	
Test of significance:					
Axis 1: $F = 1.06$, $p = 0.36$					
All canonical axes: $F = 1.19$, $p = 0.17$					

Table 5, continued.

Sweep net samples					Total
Axes	1	2	3	4	inertia
Eigenvalues	0.36	0.18	0.14	0.08	1.24
Cumulative percent variance of species data explained	28.8	43.5	55.1	61.8	
Test of significance:					
Axis 1: $F = 1.62$, $p = 0.006$					
All canonical axes: $F = 1.53$, $p = 0.028$					

All samples, presence/absence					Total
Axes	1	2	3	4	inertia
Eigenvalues	0.24	0.16	0.11	0.08	1.15
Cumulative percent variance of species data explained	21.2	34.8	44.6	51.7	
Test of significance:					
Axis 1: $F = 1.07$, $p = 0.262$					
All canonical axes: $F = 1.07$, $p = 0.361$					

Metrics					Total
Axes	1	2	3	4	variance
Eigenvalues	0.83	0.01	0.01	<0.01	1.00
Cumulative percent variance of species data explained	83.2	84.5	84.9	85.1	
Test of significance:					
Axis 1: $F = 19.83$, $p = 0.09$					
All canonical axes: $F = 4.60$, $p = 0.08$					

Table 6. Results of regressions analyzing relationships between combined core sample data and pond EV's.

	Abundance			Richness		
	r^2	p-value	relationship	r^2	p-value	relationship
depth	0.01	0.777	na	0.13	0.301	na
DO	0.19	0.211	na	0.22	0.173	na
pH	0.21	0.180	na	0.51	0.021	+
temp.	< 0.01	0.954	na	0.03	0.627	na
area	0.04	0.588	na	0.63	0.006	+

Table 7. Results of CCA's analyzing relationships between core samples and sample EV's.

Winter cores, by sample.					Total
Axes	1	2	3	4	inertia
Eigenvalues	0.31	0.18	0.16	0.09	6.13
Cumulative percent variance of species data explained	5.1	8.1	10.8	12.3	

Correlations with axes					
depth	0.49	0.01	0.26	0.28	
DO	-0.23	0.58	-0.07	0.12	
pH	-0.43	0.16	0.36	-0.19	
temperature	0.38	-0.12	0.08	0.17	
distance from margin	-0.2	-0.1	0.08	0.45	

Test of significance:

Axis 1: $F = 3.89$, $p = 0.002$

All canonical axes: $F = 2.12$, $p = 0.001$

Spring cores, by sample.					Total
Axes	1	2	3	4	inertia
Eigenvalues	0.27	0.22	0.11	0.05	5.43
Cumulative percent variance of species data explained	4.9	8.9	10.8	11.7	

Correlations with axes					
depth	0.22	0.52	0.07	0.02	
DO	-0.56	0.34	0.05	0.04	
pH	0.03	-0.25	0.45	-0.07	
temperature	-0.19	-0.42	-0.12	-0.28	
distance from margin	-0.27	0.18	0.20	0.22	

Test of significance:

Axis 1: $F = 4.37$, $p = 0.010$

All canonical axes: $F = 2.36$, $p = 0.001$

Table 8. Results of regressions analyzing relationships between core samples and sample EV's. N = 100 for all regressions.

Winter cores						
	Abundance			Richness		
	r^2	p-value	relationship	r^2	p-value	relationship
depth	0.17	<0.001		- 0.11	0.001	-
DO	0.01	0.290		na 0.01	0.405	na
pH	0.01	0.270		na 0.10	0.002	-
temp.	0.12	<0.001		- 0.03	0.100	na
dist.	0.04	0.047		- <0.01	0.520	na

Spring Cores						
	Abundance			Richness		
	r^2	p-value	relationship	r^2	p-value	relationship
depth	0.21	<0.001		- 0.07	0.010	-
DO	<0.01	0.630		na <0.01	0.633	na
pH	0.16	<0.001		+ 0.01	0.348	na
temp.	0.07	0.007		+ 0.03	0.071	na
dist.	0.09	0.003		- 0.03	0.102	na

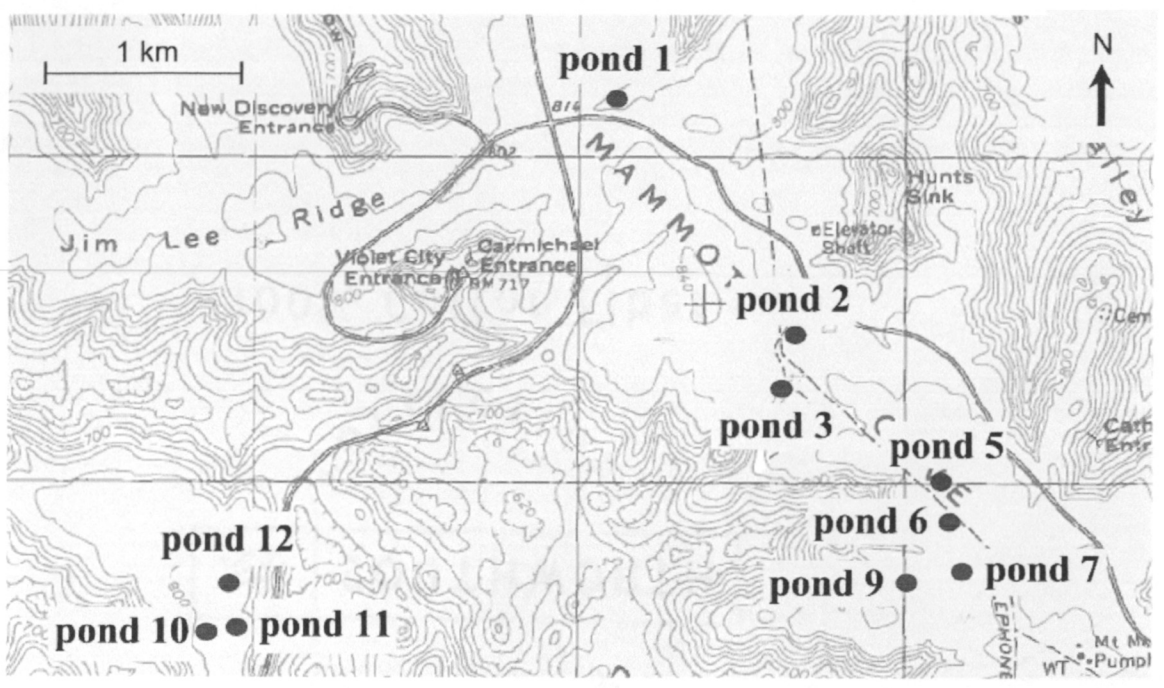


Figure 1. Location of 10 autumnal ponds in Mammoth Cave National Park, Kentucky.

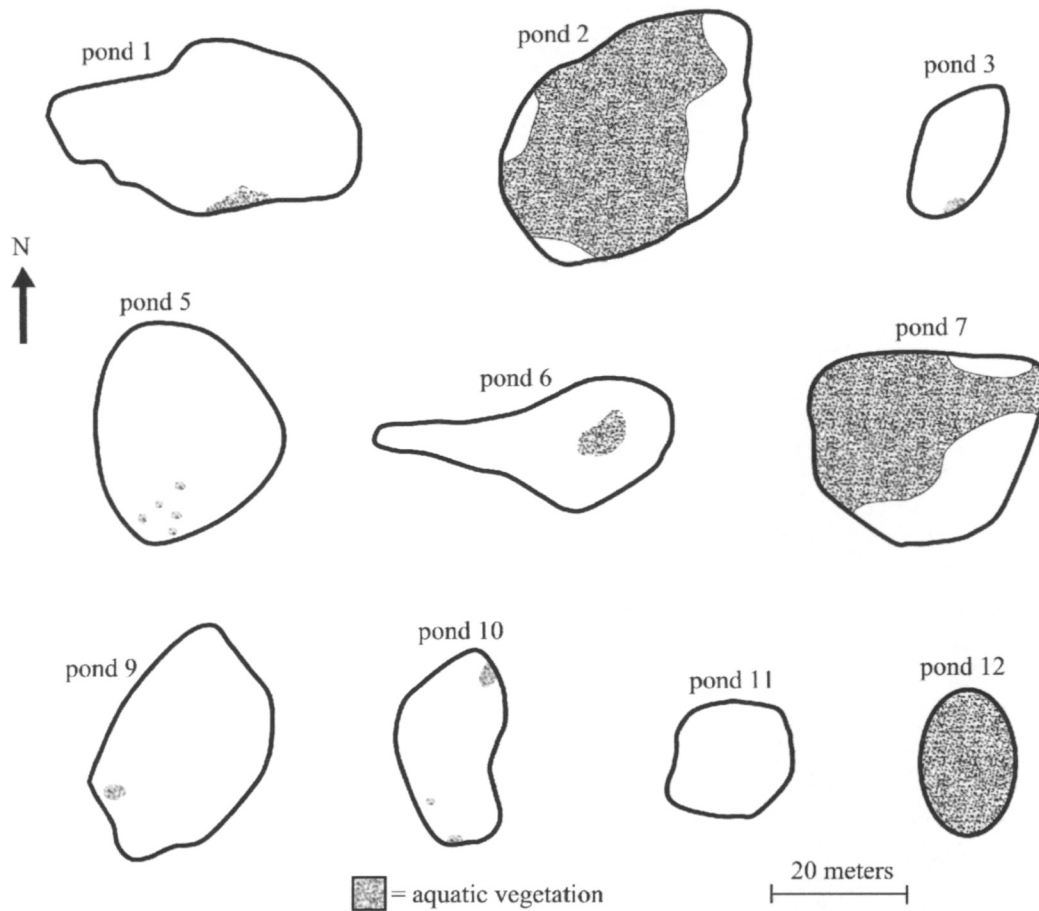


Figure 2. Physical dimensions and orientation of the 10 autumnal ponds, with aquatic vegetation shown.

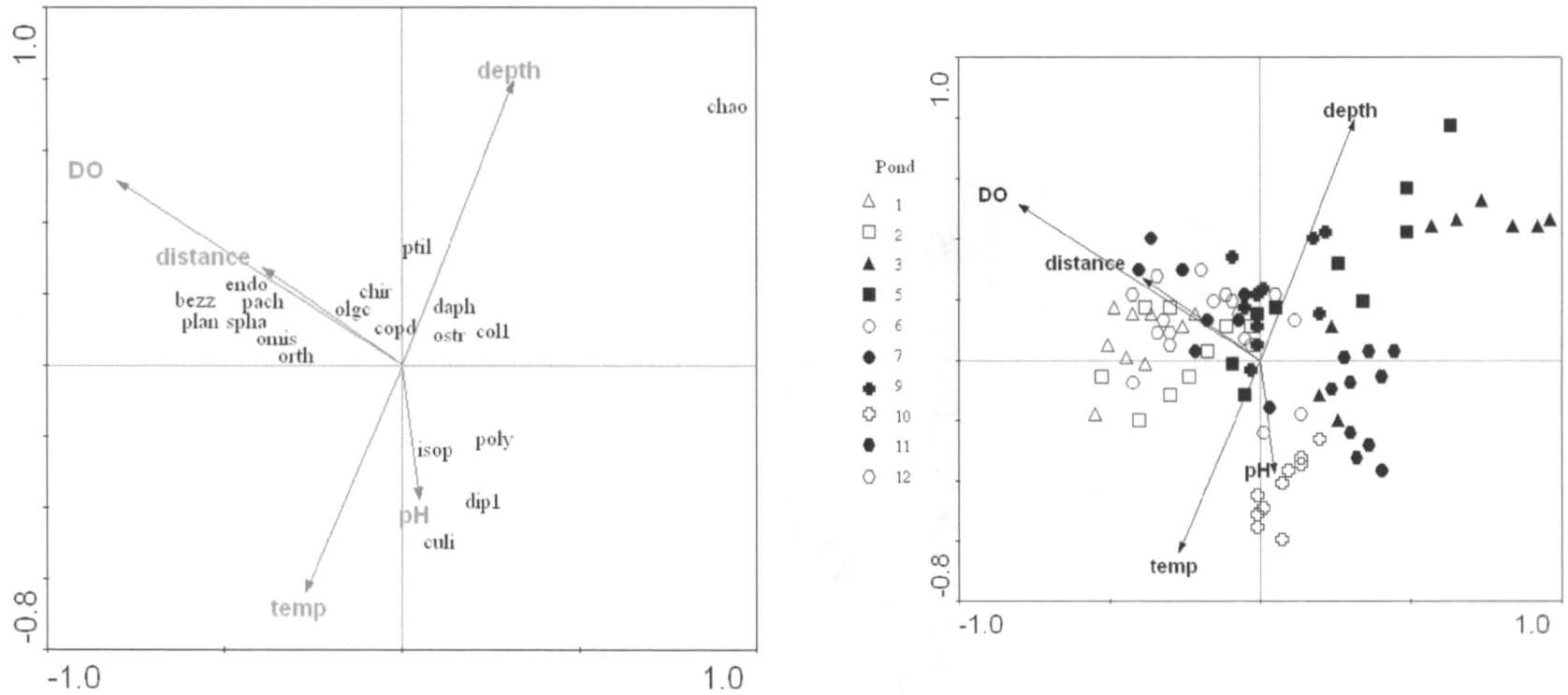


Figure 3. Within-pond CCA's using the winter core samples. Samples from shallow ponds (no samples over 0.38 m) are represented with hollow symbols. The key for taxa abbreviations can be found in Appendix A.

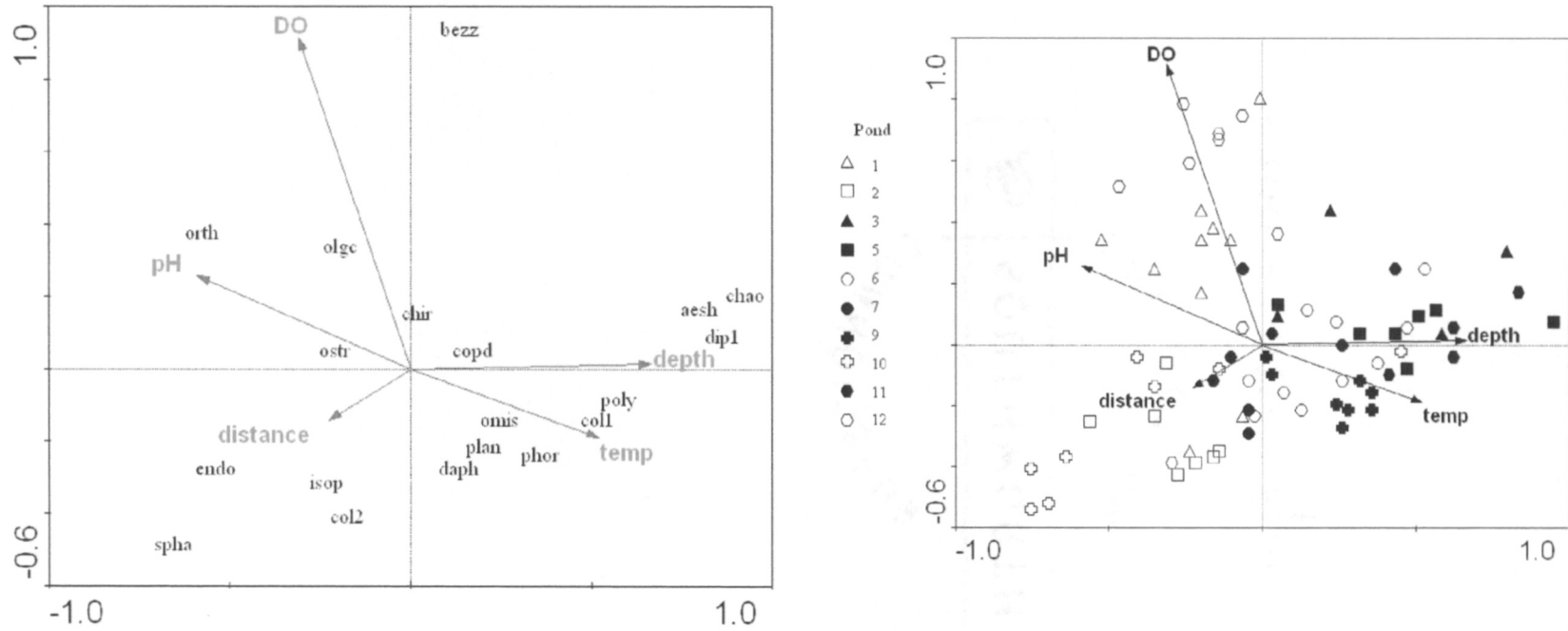


Figure 4. Within-pond CCA's using the spring core samples. Samples from shallow ponds (no samples over 0.38 m) are represented with hollow symbols. The key for taxa abbreviations can be found in Appendix A.

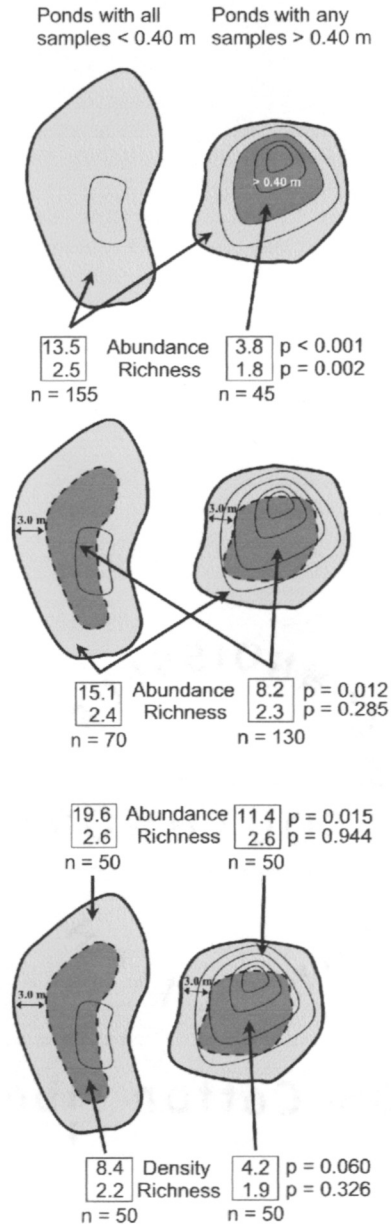


Figure 5. Mean abundance and richness from zones within the ponds. The first compares all shallow samples (less than 0.40 m) to all deep samples (0.40 m or more). The second compares samples taken near the pond margin (within 3.0 m) to the central samples (over 3.0 m). The third compares the near-margin samples of a shallow pond to near-margin samples of a deep pond, and central samples of a shallow pond to central samples from a deep pond.

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Appendix A

Macroinvertebrates collected from 10 autumnal ponds, ordered by the number of ponds in which they occurred.

taxa	abbr.	pond occ. (N = 10)	core occ. (N = 200)	sweep occ. (N = 10)	total sampled
Copepoda	copd	10	63	8	1386
Isopoda, Asellidae <i>Caecidotea</i> sp.	isop	10	68	10	10177
Oligochaeta	olgc	10	67	7	395
Ostracoda, Podocopida	ostr	10	61	8	558
Anomopoda, Daphniidae	daph	9	19	9	2411
Coleoptera, unknown #1	col1	8	25	2	35
Diptera, Chironominae, <i>Chironomus</i>	chir	8	34	8	769
Coleoptera, Dytiscidae, <i>Hydroporus</i> sp.	hydp	6	0	6	31
Diptera, Chaoboridae <i>Chaoborus</i> sp.	chao	6	8	6	252
Diptera, Chironominae, <i>Polypedilum</i>	poly	6	20	6	123
Diptera, Orthocladinae	orth	6	16	5	493
Hemiptera, Corixidae	corx	6	0	6	20
Coleoptera, Dytiscidae, <i>Acilius</i> sp.	acil	5	0	5	8
Diptera, Ceratopogonidae, <i>Bezzia</i> sp.	bezz	5	4	3	13
Diptera, Chironominae, <i>Omisus</i>	omis	5	27	5	235
Diptera, Tanypodinae	tany	5	0	4	5
Planorbidae, <i>Planorbula armigera armigera</i>	plan	4	10	4	121
Coleoptera, Dytiscidae, <i>Ilybius</i> sp.	ilyb	4	0	4	16
Odonata, Libellulidae, <i>Pachydiplax</i> sp.	pach	4	1	3	15
Coleoptera, Dytiscidae, <i>Copelatus</i> sp.	copl	3	0	3	6
Coleoptera, Hydrophilidae, <i>Hydrobiomorpha</i> sp.	hydb	3	0	3	3
Diptera, Chironominae, <i>Endochironomus</i>	endo	3	11	3	290
Diptera, unknown #1	dip1	3	5	0	10
Tricoptera, Phryganeidae, <i>Ptilostomis</i> sp.	ptil	3	1	3	7
Coleoptera, Dytiscidae, <i>Hydaticus</i> sp.	hydt	2	0	2	7
Coleoptera, Dytiscidae, <i>Rhantus</i> sp.	rhan	2	0	2	2
Coleoptera, unknown #2	col2	2	2	0	3
Diptera, Culicidae <i>Culex</i> sp.	culi	2	6	1	554
Odonata, Aeshnidae <i>Aeshna</i> sp.	aesh	2	1	1	4
Sphaerium, Sphaeridae, <i>Sphaerium occidentale</i>	spha	1	14	1	155
Coleoptera, Dytiscidae, <i>Coptotomus</i> sp.	copt	1	0	1	1
Coleoptera, unknown #3	col3	1	0	1	3
Diptera, Phoridae	phor	1	1	0	2
Ephemeroptera, Baetidae, <i>Calibaetis</i> sp.	cali	1	0	1	4
Megaloptera, Corydalidae, <i>Chauliodes</i> sp.	chau	1	0	1	3