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USE OF MACROINVERTEBRATES TO IDENTIFY CULTIVATED WETLANDS IN THE PRAIRIE POTHOLE REGION

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Abstract: We evaluated the use of macroinvertebrates as a potential tool to identify dry and intensively farmed temporary and seasonal wetlands in the Prairie Pothole Region. The techniques we designed and evaluated used the dried remains of invertebrates or their egg banks in soils as indicators of wetlands. For both the dried remains of invertebrates and their egg banks, we weighted each taxon according to its affinity for wetlands or uplands. Our study clearly demonstrated that shells, exoskeletons, head capsules, eggs, and other remains of macroinvertebrates can be used to identify wetlands, even when they are dry, intensively farmed, and difficult to identify as wetlands using standard criteria (i.e., hydrology, hydrophytic vegetation, and hydric soils). Although both dried remains and egg banks identified wetlands, the combination was more useful, especially for identifying drained or filled wetlands. We also evaluated the use of coarse taxonomic groupings to stimulate use of the technique by nonspecialists and obtained satisfactory results in most situations.

Key Words: aquatic invertebrate signatures, delineation, macroinvertebrates, prairie potholes, wetland identification

INTRODUCTION

Wetlands in the United States have been the focus of considerable controversy since European settlement. Initially perceived as wastelands that produced mosquitoes and other insects associated with human diseases and as impediments to agricultural production, federal policies targeted wetlands for conversion to cropland and other land uses. By the 1950s, growing concern over the loss of prairie wetlands and their importance to waterfowl and migratory birds led to the enactment in 1958 of the small wetlands acquisition program (Public Law 87–383). Increasing interest and knowledge of wetland functions, coupled with concern over continuing wetland losses, stimulated additional interest in protecting wetlands. Wetland protection increased in 1972 with the passage of the Federal Water Pollution Control Act (Public Law 92–500), in 1977 under amendments to Section 404 of the Federal Water Pollution Control Act (Clean Water Act; Public Law 95–217), and in 1985 under the Food Security Act (Public Law 99–198). Wetlands originally comprised about 9% of the land surface and about 90 million ha in the United States; about half of that area had been drained or converted to other land uses by the mid-1980s (National Research Council 1995). Today, wetlands are the only ecosystems that are regulated on both public and private lands in the United States.

To support national needs, several manuals have been developed to help federal regulators identify and delineate wetlands. The first such manual was developed by the U.S. Army Corps of Engineers (USACE) in 1987 (U.S. Army Corps of Engineers 1987). In 1989, an interagency manual (Federal Interagency Committee for Wetlands Delineation 1989) was developed by the USACE, the U.S. Fish and Wildlife Service, the Environmental Protection Agency (EPA), and the U.S. Department of Agriculture (USDA). The 1989 interagency manual was strongly criticized because it was perceived as designating areas as wetland that should be classified as upland (National Research Council 1995). Hence, a revised manual was prepared in 1991, but it was criticized for excluding many important wetlands and was not adopted. To further complicate the development of a uniform scientific definition of wetlands, the USDA developed a separate manual for agricultural wetlands relying on definitions established under the 1985 Food Security Act (U.S. Department of Agriculture 1994). With neither of the wetland identification manual versions proving satisfactory and a separate manual being used for agricultural wetlands, confusion existed over how to identify and delineate wetlands. As a result, Congress requested in 1993 that the EPA ask the National Research Council (NRC) to form a committee to evaluate the scientific basis for identifying and delineating wetlands and to assess the adequacy of existing manuals. The NRC report made a number of recommendations, including the need to develop a new manual that would serve the broad needs of all federal regulators and be based on scientifically credible procedures that would accurately identify wetlands and avoid misclassifications (National Research Council 1995).

Three features (wetland hydrology, hydric soils, and hydrophytic vegetation) are used to define wetlands according to each of the three wetland definitions currently used in the United States—those of the U.S. Army Corps of Engineers (1987), the 1985 Food Security Act (Public Law 99–198), and the U.S. Fish and Wildlife Service (Cowardin et al. 1979). Current indicators of wetland hydrology (watermarks, drift lines, sediment deposits, visual observation of saturation, etc.) are much more variable on a short time scale than are the indicators of hydric soils (U.S. Department of Agriculture 1996) and hydrophytic vegetation (Reed 1988), so that hydric soil and vegetation indicators often are used to infer wetland hydrology (National Research Council 1995). Identification of wetlands within agricultural landscapes using current indicators of wetland hydrology, hydric soils, and hydrophytic vegetation is often difficult in the Prairie Pothole Region (PPR) of North America because indicators of wetland hydrology are often destroyed, soils are often disturbed by tillage, and/or plant communities may have been artificially altered or removed by farming practices (U.S. Army Corps of Engineers 1987). The problem is exacerbated during drought years by increased agricultural activity within wetland basins. A need exists for additional indicators that can be used to identify wetlands during periods of drought or when basins have been disturbed by intensive agricultural activity.

The recalcitrant remains of macroinvertebrates (e.g., shells, chitinous exoskeletons, and head capsules), resistant eggs, and aestivating adults or immatures may offer a new tool for determining the presence or absence of wetland hydrology. Most macroinvertebrate taxa are specific to particular hydrologic regimes that define wetland classes (Wiggins et al. 1980, Pennak 1989, Schneider and Frost 1996, Euliss et al. 1999). Further, many taxa are ubiquitous in wetlands but are not found elsewhere. Moreover, their remains may persist in wetlands for long periods and are not easily destroyed by mechanical tillage. Hence, they provide time-integrated information on wetland hydrology useful in identifying wetlands.

To test the feasibility of using macroinvertebrate remains as a wetland identification tool, we initiated research in 1992 with the following objectives. First, we wanted to determine if recalcitrant remains of invertebrates could be used to identify temporary and seasonal wetlands and separate them from the adjacent upland within intensively tilled agricultural fields. We chose temporary and seasonal wetlands because these two wetland classes (Stewart and Kantrud 1971) are most commonly farmed. Second, we wanted to determine if macroinvertebrate recalcitrant remains could be used to separate with some confidence seasonal wetlands from temporary wetlands. We conducted our study on cultivated wetlands in the glaciated drift prairie of North Dakota, South Dakota, and Minnesota, an area of extensive agricultural activity.

METHODS

Using National Wetlands Inventory (NWI) (Wilen and Bates 1995) wetland designations, we sampled 32 temporary and 32 seasonal wetlands in 1992. These wetlands were randomly selected from agricultural fields within 10.4-km^2 plots monitored by the U.S. Fish and Wildlife Service to estimate waterfowl recruitment using the mallard model (Cowardin et al. 1988). However, we dropped 2 temporary wetlands from our sample because we determined that our field crew had not collected samples from the correct location. We focused on the glaciated drift prairie in North Dakota, South Dakota, and Minnesota because it has been extensively developed for agricultural production and contains many seasonal and temporary wetlands. Only wetlands that were dry and intensively farmed when visited were included in this study. If on our initial site visit, a wetland was found to have been artificially drained, we excluded that wetland from our sample and selected an alternate wetland from the sample universe described above. Our goal was to evaluate the technique on the shortest hydroperiod wetlands in the PPR: those that were highly modified by agriculture and were difficult or impossible to identify using conventional techniques during dry periods. In August and September, we collected 12 soil samples at each site: six from the deepest portion of the wetland basin and six from the adjacent upland. We used a laser plane surveying instrument to locate the deepest portion of each wetland. We also used the laser plane to determine the elevation at which each wetland would overflow during flooding. We then defined 3 transects that radiated from the deepest portion of each wetland to the adjacent upland along random compass bearings. Four soil samples were collected from each transect; duplicate 500-cm^3 wetland samples were collected 1 m from the deepest portion of each wetland, and duplicate 500-cm^3 upland samples were collected at an elevation of 15 cm above the overflow elevation of each wetland. We designed this sampling scheme to ensure that samples from only wetland and upland habitats were collected. Soil samples were collected by coring 10 cm deep with a 8-cm-diameter coring device. Samples were frozen until processed in our laboratory.

We examined the soil samples in two ways. First, we visually examined one duplicate of the three wetland and the three upland soil samples from each wetland for recalcitrant remains of invertebrates under a low-magnification dissecting scope after concentrating remains by sieving through a 0.5-mm-mesh screen. Second, we incubated the remaining soil samples in 37.9-L aquaria under standardized light (12-hour day length), specific conductance (700 μS cm^{-1}), and temperature regimes (four weeks at 8°C followed by four weeks at 22°C). In order to promote the emergence of the maximum number of taxa, we used the above dual temperature regime meant to simulate temperatures of wetlands following early spring snowmelt and after major summer precipitation events. At the end of the first 4-week incubation, we siphoned the contents of each aquarium through a 0.5-mm-mesh screen and returned the sieved water to its original aquarium for a second incubation at the alternate temperature. Invertebrates retained by the 0.5-mm-mesh screen during each 4-week incubation were combined and processed as a single sample. Invertebrates were sorted into taxonomic groupings according to Pennak (1989) and enumerated from both the visually examined field samples and our incubated aquarium samples, hereafter termed field and incubated samples, respectively.

Statistical Methods

We calculated taxon richness and counts of individuals by taxon, and taxon richness and counts of individuals weighted by the affinity of each taxon for wetlands. We determined the wetland association categories for each invertebrate taxon based on autecological relationships in published sources (Barnes 1968, Borror et al. 1981, Clarke 1981). The categories and weights we used were as follows: wetland obligate (taxon occurs only in wetlands), 1.0; facultative wetland (taxon occurs usually in wetlands), 0.75; facultative (taxon occurs regularly in both wetlands and uplands), 0.5; facultative upland (taxon occurs usually in uplands), 0.25; and upland obligate (taxon occurs only in uplands), 0.0. Because of the patchy distribution of aquatic invertebrates (Elliott 1977), we took a logarithmic transformation of the counts and used the variable log(count + 1), hereafter termed LogCount.

To facilitate use by those not very familiar with invertebrate identification, we also did an analysis with a simplified taxonomy. For this purpose, we combined into single groupings all planorbid snail shells, lymnaid snail shells, physid snail shells, cladoceran resting eggs (ephippia), ostracod shells, and trichopteran cases for the visually examined field samples, as well as all Cladocera, Copepoda, Ostracoda, Anostraca, and Conchostraca individuals for the incubated samples.

Data from the three transects were summed to provide a single value for each wetland and another for the adjacent upland. We computed means and standard errors of number of taxa and LogCount, unweighted and weighted by wetland-obligate status, for field and incubated samples, within location (upland, wetland), and by wetland class (seasonal, temporary). We tested for differences between upland and wetland sites and between wetland classes with a randomized-incomplete block analysis of variance using PROC MIXED (SAS Institute 1997), where habitat type (upland, temporary wetland, seasonal wetland) was the explanatory variable and sites were blocks. The response variables were number of taxa and LogCount; the explanatory variable was habitat type (upland, temporary wetland, seasonal wetland). We also computed least-squares means for each response variable by habitat type (SAS Institute 1997); separation among habitat types was performed using Fisher's protected LSD procedure following significant F-tests in ANOVAs (Milliken and Johnson 1984). This procedure was performed for both field and incubated samples and for complete and simplified taxonomies.

To classify wetland sites, we found a straight line in the Taxon Richness—LogCount plane (i.e., a two dimensional, flat surface) that best distinguished upland from wetland sites on the basis of those two variables (Figure 1). This was done through an iterative trial-and-error procedure by successively calculating lines and then determining the number of misclassified sites: the number of wetland sites below that line plus the number of upland sites above the line. A line that produced the minimum number of misclassifications was selected. This was done separately for the field and incubated samples. We chose this method because of its simplicity and the fact that the data did not meet assumptions of other straightforward classification methods, such as linear discriminant function analysis.

RESULTS

Comparison of Wetland and Upland Samples

Field Samples. We identified 46 categories of invertebrate remains in our field samples (Table 1), 6 of which were used in our simplified taxonomy (Table 2). Average values of taxon richness and LogCount for field samples differed markedly among the three habitat types (upland, temporary wetland, seasonal wetland) regardless of whether or not weighting was done or if the simplified taxonomy was used (Table 3). When unweighted, taxon richness ($F_{2,60} = 26.21$; $P < 0.0001$) differed among the three habitat types with

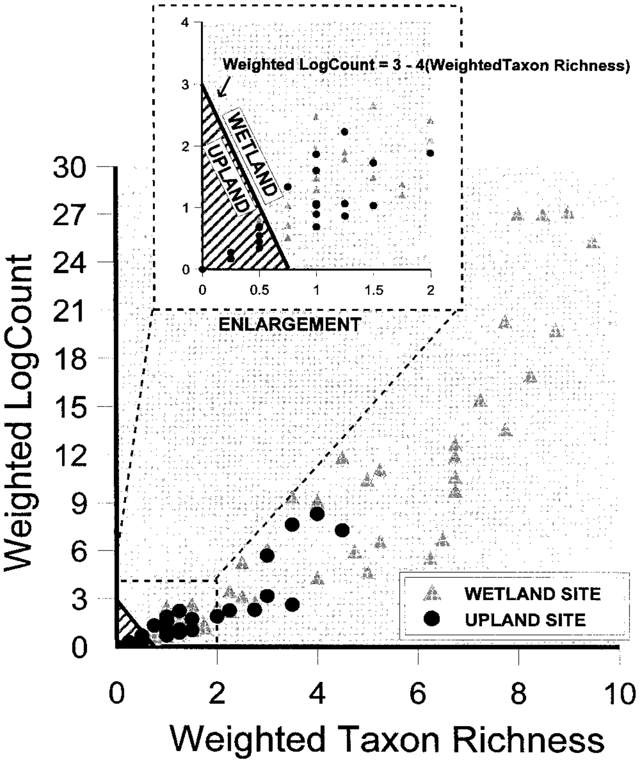

Figure 1. Relationship of LogCount and the number of invertebrate taxa, weighted by habitat affinity, for visually derived field data using compete taxonomy for 62 intensively farmed temporary and seasonal wetlands in the Prairie Pothole Region. The line, weighted LogCount = 3–4 (weighted taxon richness), separated wetland and upland sites with the minimal number of classification errors (21.8%). Thirty upland observations are hidden in the lower, lefthand corner.

both wetland types being similar to each other ($P = 0.34$) but not ($P < 0.0001$) to the upland. The unweighted LogCount ($F_{2,60} = 17.85$; $P < 0.0001$) also differed by habitat type with wetland types differing from upland ($P < 0.0001$) and marginally from each other ($P = 0.058$). Taxon richness for the weighted samples also differed among habitat types ($F_{2,60} = 32.41$; $P < 0.0001$), with both wetland types being fairly similar to each other ($P > 0.09$) but not to the upland ($P < 0.0001$). The weighted LogCounts also differed by habitat type ($F_{2,60} = 21.06$; $P < 0.0001$), but each was statistically unique ($P < 0.03$). Using the simplified taxonomy, each of the habitat types were statistically unique, with both taxon richness ($F_{2,60} = 26.93$; $P < 0.0001$) and LogCount ($F_{2,60} = 26.04$; $P < 0.0001$) differing among the three habitat types.

Incubated Samples. We successfully incubated invertebrates representing 15 taxa (Table 4), which we grouped into 5 taxa in our simplified taxonomy (Table 5). For our incubated samples, we found that the differences in taxon richness and LogCount among the three habitat types (upland, temporary wetland, seasonal wetland) were even greater than found for the field samples, regardless of whether or not weighting was done or the simplified taxonomy used (Table 6). Using unweighted data, the three habitat types differed from one another for both taxon richness ($F_{2,60} = 60.23$; $P < 0.0001$) and LogCount ($F_{2,60} = 42.33$; $P < 0.0001$). Similarly for the weighted samples, we found that both taxon richness ($F_{2,60} = 60.56$; $P < 0.0001$) and LogCount ($F_{2,60} = 42.19$; $P < 0.0001$) differed among habitat types. In all cases for both weighted and unweighted samples, each of the habitat types was statistically unique ($P < 0.05$). The results for the analysis using the simplified taxonomy were similar for taxon richness and LogCount, with a large difference among habitat types for LogCount ($F_{2,60} = 48.26$; $P < 0.0001$) and each of the habitat types being distinctive ($P < 0.05$).

Classification of Sites

For the field data with the complete taxonomy, we found that when both variables were weighted by wetland affinity, the line that separated the data with the fewest (27/124 = 21.8%) classification errors was defined by:

$$\text{LogCount} = 3\text{–}4(\text{Taxon Richness})$$

Most of the errors (25 of 27) represented upland sites classified as wetlands (Figures 1 and 2). The simplified taxonomy produced a slightly higher error rate; 29 of 124 (23.4%) sites were misclassified. Among the numerous lines that yielded the best results was the same one generated from the complete taxonomy analysis: LogCount = 3–4(Taxon Richness). Ten upland sites were misclassified as wetland, and 19 wetland sites (13 temporary and 6 seasonal) were misclassified as upland. In contrast to the complete taxonomy, we found that using the simplified taxonomy correctly classified more of the upland sites and fewer of the wetlands.

For the aquarium data, we found satisfactory the simple rule that classified sites as wetland if either number of taxa > 0 or LogCount > 0. This rule, with the complete taxonomy, yielded seven wetland sites (six temporary and one seasonal) classified as upland, and seven upland sites classified as wetland, for an overall error rate of 14/124 = 11.3%. With the simplified taxonomy, the rule misclassified the same sites as with the complete taxonomy, as well as an additional seasonal wetland site that was misclassified as upland; the overall error rate was 15/124 = 12.1%.

DISCUSSION

This study clearly shows that shells, exoskeletons, head capsules, eggs, and other remains of macroinver-

Table 1. Evidence type used, habitat affinity (HA), frequency of occurrence (F), and mean count of taxa in field samples from upland sites, temporary wetland sites, and seasonal wetland sites. OW = Obligate Wetland, FW = Facultative Wetland, FA = Facultative, FU = Facultative Upland, OU = Obligate Upland.

			Upland		Temporary		Seasonal	
Taxon	Evidence Type	HA	F(%)	Mean	F(%)	Mean	F(%)	Mean
Gastropoda	Fragments	FA	24.2	0.34	40.0	1.10	53.1	6.03
Planorbidae	Shells	OW	8.1	0.44	6.7	0.13	15.6	1.06
Helisoma	Shells	OW	0.0	0.00	6.7	0.13	6.2	1.47
Arminger crista L.	Shells	OW	1.6	3.23	6.7	1.13	6.2	1.59
Promenetus exacuous Say	Shells	OW	0.0	0.00	0.0	0.00	6.2	1.53
Gyralus	Shells	OW	8.1	0.48	30.0	2.27	40.6	6.34
Promenetus umbilicus Cockerell	Shells	OW	0.0	0.00	10.0	0.13	9.4	3.47
Planorbula	Shells	OW	1.6	0.23	3.3	0.07	3.1	0.03
Lymnaeidae	Shells	OW	12.9	0.68	40.0	30.37	56.2	30.16
Physidae	Shells	OW	0.0	0.00	10.0	0.47	15.6	5.09
Aplexa hyphorum L.	Shells	OW	0.0	0.00	6.7	0.20	9.4	8.25
Truncatillidae	Shells	OW	8.1	0.42	6.7	0.17	9.4	1.87
Cladocera	Eggs	OW	4.8	0.05	36.7	10.67	43.7	265.44
Ostracoda	Shells	OW	0.0	0.00	6.7	2.07	12.5	2.34
Conchostraca	Shells	OW	0.0	0.00	3.3	0.03	3.1	0.59
Annelida	Remains	FU	11.3	0.24	6.7	0.10	3.1	0.03
Oligochaeta (terrestrial)	Remains	OU	9.7	0.18	10.0	0.20	6.2	0.06
Nematoda	Remains	FU	3.2	0.06	3.3	2.77	3.1	0.47
Nematomorpha	Remains	FW	1.6	1.23	3.3	0.03	3.1	0.06
Hemiptera (terrestrial)	Remains	OU	1.6	0.16	0.0	0.00	0.0	0.00
Corixidae	Remains	FW	0.0	0.00	6.7	0.13	9.4	0.53
Notonectidae	Remains	FW	0.0	0.00	0.0	0.00	3.1	8.94
Pleidae	Remains	FW	0.0	0.00	6.7	0.97	0.0	0.00
Trichoptera	Cases	OW	0.0	0.00	3.3	0.07	12.5	0.12
Diptera Larvae	Remains	FU	25.8	1.56	43.3	2.40	21.9	0.93
Chironomidae Larvae	Remains	FW	0.0	0.00	13.3	1.27	18.7	3.28
Diptera (Adult)	Remains	OU	9.7	0.23	10.0	0.13	3.1	0.03
Hymenoptera	Remains	OU	8.1	0.76	10.0	0.17	6.2	0.12
Hymenoptera	Eggs	OU	1.6	0.10	0.0	0.00	0.0	0.00
Homoptera	Remains	OU	3.2	0.06	0.0	0.00	0.0	0.00
Homoptera	Eggs	OU	3.2	0.37	0.0	0.00	0.0	0.00
Odonata (Larvae)	Remains	OW	1.6	0.02	6.7	0.07	6.2	0.06
Lepidoptera	Remains	OU	6.4	0.06	3.3	0.03	9.4	0.09
Orthoptera	Remains	OU	1.6	1.61	3.3	0.10	6.2	0.06
Thysanoptera	Remains	OU	0.0	0.00	3.3	0.03	9.4	0.09
Unidentified Coleoptera	Remains	FA	30.6	0.55	36.7	0.83	34.4	0.97
Coleoptera (terrestrial)	Remains	OU	50.0	1.53	33.3	0.83	46.9	1.03
Hydrophilidae	Remains	FW	0.0	0.00	16.7	0.23	18.7	0.47
Berosus	Remains	FW	0.0	0.00	13.3	0.20	25.0	0.28
Hydrochus	Remains	FW	0.0	0.00	10.0	0.13	6.2	0.06
Dytiscidae	Remains	FW	1.6	0.03	20.0	0.30	21.9	0.44
Haliplidae	Remains	FW	1.6	0.02	0.0	0.00	18.7	0.25
Collembola	Remains	FU	3.2	0.03	6.7	0.07	6.2	0.06
Acari	Remains	FA	4.8	0.06	10.0	0.37	6.2	0.12
Araneida	Remains	FU	0.0	0.00	6.7	0.10	6.2	0.09
Chilopoda	Remains	OU	3.2	0.03	0.0	0.00	0.0	0.00

Table 2. Simplified taxa evidence type used, habitat affinity (HA), frequency of occurrence (F), and average count in field samples from upland sites, temporary wetland sites, and seasonal wetland sites (OW = Obligate Wetland).

			Upland		Temporary		Seasonal	
Taxon	Evidence Type	HA	F(%)	Mean	F(%)	Mean	F(%)	Mean
Planorbidae	Shells	OW	11.3	1.47	33.3	3.87	50.0	15.50
Lymnaeidae	Shells	OW	12.9	0.68	40.0	30.37	56.2	30.16
Physidae	Shells	OW	0.0	0.00	16.7	0.67	21.9	13.34
Cladocera	Eggs	OW	4.8	0.05	36.7	10.67	43.75	265.44
Ostracoda	Shells	OW	0.0	0.00	6.7	2.07	12.5	2.34
Trichoptera	Cases	OW	0.0	0.00	3.3	0.07	12.5	0.12

tebrates can serve as indicators of wetland hydrology, even when the basins are being intensively farmed, as commonly occurs during dry periods in the PPR and elsewhere. The year we collected our samples, 1992, was the last year of a drought comparable in severity to that of the 1930s (Winter and Rosenberry 1998). All of the temporary and most of the seasonal wetlands in our study were tilled and planted to small grains or row crops when we sampled them; had they not been identified by NWI during previous periods of abundant water, most of the wetlands would have been nearly invisible and difficult, if not impossible, to identify using current indicators of hydrology, soils, and hydrophytes. The cryptic nature of farmed wetlands was reflected in the difficulty our field crew had finding specific basins to sample. However, we identified the majority of the wetlands based solely on invertebrate signatures and cultured invertebrates remaining in the soils.

In the summer of 1994, we revisited each of the sites misclassified by our techniques. In all 25 situations where we falsely classified upland sites as wetland, we found that errors in our interpretation of the surrounding landscape were responsible for the misclassifications. In 23 sites, we found specific topographic features (e.g., road beds functioning as dams) that, during periods of high water, would allow the wetland to flood the area where we collected our samples; thus these ‘‘upland’’ samples were actually collected from within the wetlands’ boundaries. In the other two sites, adjacent wetlands would periodically backflood the wetlands sampled by backing water up and over the elevation at which the sample wetland would normally overflow. Wetlands throughout much of the semi-arid PPR lack surface outlets (Eisenlohr 1972), but adjacent basins often do coalesce, especially during periods of high water as occurred following the historic 1993 flood throughout the PPR. However, most of the misclassifications of upland sites (i.e., upland samples containing aquatic invertebrate remains) were due to secondary ponding from elevated road beds, which are numerous throughout the PPR.

Our 1994 visit to the misclassified sites occurred after the historic precipitation event in 1993, which refilled wetlands to record depths throughout the PPR and provided us with a much better view of wetland boundaries, the topographic relationships between adjacent basins that caused them to coalesce, and the impact of elevated road beds that functioned as dams and impounded water above historic pool levels. Had we correctly interpreted the topographic surroundings of each of the sites we sampled, our error rate would have been much lower. Hence, we believe that our methods would be more accurate than other available wetland indicators. The technique should work better in less disturbed habitats and in wetlands with more permanent water regimes because they contain more perennial and diverse invertebrate communities (Driv-

Table 3. Adjusted marginal means and standard errors (in parentheses) of numbers of species from field samples and LogCount; unweighted (all taxa), weighted (all taxa), and with simplified taxonomy. Means within column not sharing the same superscript are significantly different (*P* = 0.05).

	Unweighted		Weighted		Simplified taxonomy	
Habitat	Number of Species	LogCount	Number of Species	LogCount	Number of Species	LogCount
Upland	2.53^{a}	3.03^{a}	0.85^{a}	1.08^{a}	0.28^{a}	0.47^{a}
	(0.39)	(0.82)	(0.28)	(0.67)	(0.17)	(0.47)
Temporary	4.94^{b}	7.20^{b}	2.97^{b}	4.94^{b}	1.35^{b}	3.28^{b}
	(0.51)	(1.15)	(0.38)	(0.96)	(0.22)	(0.67)
Seasonal	5.91^{b}	10.46^{c}	3.91^{b}	8.00^{c}	1.97^{c}	5.19^{c}
	(0.49)	(1.12)	(0.36)	(0.93)	(0.22)	(0.64)

Table 4. Taxa, habitat affinity, frequency of occurrence (F), and average number incubated from samples from upland sites, temporary wetland sites, and seasonal wetland sites (FW = Facultative Wetland, OW = Obligate Wetland).

Taxon	Habitat Affinity	Upland		Temporary		Seasonal	
		F(%)	Mean	F(%)	Mean	F(%)	Mean
Cladocera							
Ceriodaphnia sp.	OW	1.6	0.16	13.3	55.83	15.7	14.87
Daphnia sp.	OW	3.2	0.03	6.7	7.60	15.6	32.16
Macrothrix sp.	OW	1.6	0.34	6.7	14.93	0.0	0.0
Moina sp.	OW	4.8	1.06	53.3	31.60	62.5	96.16
Simocephalus sp.	OW	0.0	0.00	0.0	0.00	12.5	78.12
Ostracoda	OW	1.6	0.05	26.7	1.73	46.9	8.16
Copepoda							
Calanoida	OW	0.0	0.00	16.7	0.57	12.5	1.84
Cyclopoida	OW	0.0	0.00	0.0	0.00	3.1	0.06
Anostraca							
Branchinecta lindahli Packard	OW	1.6	0.05	23.3	4.20	31.2	4.87
Streptocephalus dorothae Mackin	OW	0.0	0.00	0.0	0.00	6.2	0.12
Conchostraca							
Eulimnadia sp.	OW	3.2	0.06	16.7	0.50	18.7	1.09
Aquatic Oligochaeta	OW	0.0	0.00	0.0	0.00	3.1	0.03
Diptera							
Chironomidae	FW	0.0	0.00	0.0	0.00	3.1	0.03
Coleoptera							
Berosus fraturnus LeConte (adults)	FW	0.0	0.00	3.3	0.07	3.1	0.03
Berosus fraturnus LeConte (larvae)	OW	0.0	0.00	3.3	0.07	0.0	0.00

er 1977, Euliss et al. 1999). While other currently available indicators are usually adequate for identifying wetlands when they contain water, invertebrate remains provide additional information, which should strengthen identification decisions.

The study also suggests that simple visual examination of soil samples collected from basins using a simplified taxonomy is often sufficient to identify most temporary and seasonal wetlands in agricultural fields. However, in cases where wetlands cannot be positively identified, incubation of samples or the use of a more detailed taxonomy may be used to corroborate or refute results obtained with other methods. Incubation of the samples in aquaria, although logistically more challenging than visual inspection, provided the clearest and most straightforward separation of wetland and upland sites. The rule was extremely simple: if aquatic invertebrates were cultivated in the aquarium incubations, assign the site as wetland. Using this rule, we failed to identify only 7 out of 62 wetlands. However, even those apparent misclassifications provided valuable information on the classification and appear to reflect accurately the history of each specific site. The absence of viable aquatic invertebrate eggs in the soil samples may suggest that the wetland has ceased to function as a wetland. Four of the wetland sites that

Table 5. Simplified taxa, habitat affinity, frequency of occurrence (F), and average count incubated from samples from upland sites, temporary wetland sites, and seasonal wetland sites (OW = Obligate Wetland).

Taxon	Habitat Affinity	Upland		Temporary		Seasonal	
		F(%)	Mean	F(%)	Mean	F(%)	Mean
Cladocera	OW	8.1	1.11	60.0	95.03	75.0	143.19
Ostracoda	OW	1.6	0.05	26.7	1.73	46.9	8.16
Copepoda	OW	0.0	0.00	16.7	0.57	15.6	1.91
Anostraca	OW	1.6	0.05	23.3	4.20	31.2	5.00
Conchostraca	OW	3.2	0.06	16.7	0.50	18.7	1.09

Table 6. Adjusted marginal means and standard errors (in parentheses) of numbers of species incubated from samples and LogCount; unweighted (all taxa), weighted (all taxa), and with simplified taxonomy. Means within column not sharing the same superscript are significantly different ($P = 0.05$).

	Unweighted		Weighted		Simplified Taxonomy	
Habitat	Number of Species	LogCount	Number of Species	LogCount	Number of Species	LogCount
Upland	0.19^a	0.27^a	0.19^a	0.27^a	0.15^a	0.21^a
	(0.16)	(0.44)	(0.16)	(0.44)	(0.11)	(0.33)
Temporary	1.72^b	3.96^b	1.73^b	3.96^b	1.44^b	3.47^b
	(0.20)	(0.76)	(0.20)	(0.59)	(0.15)	(0.45)
Seasonal	2.34^c	6.31^c	2.32^c	6.29^c	1.88^b	5.15^c
	(0.20)	(0.57)	(0.20)	(0.57)	(0.14)	(0.43)

were classified as upland (i.e., wetland samples from which we were unable to culture aquatic invertebrates in the aquarium incubations) turned out to be drained wetlands from which we found recalcitrant remains of aquatic invertebrates in the visual evaluation. However, these seemingly contradictory results actually contrast the current versus historic condition and function of each of the drained wetlands; they contained invertebrate signatures detected in the visual field data indicating that they were once wetlands, but they apparently no longer contained viable invertebrate eggs and hence appear to function currently as uplands. In this study, we found no evidence to suggest that intensive land use reduced our ability to identify wetlands within agricultural landscapes, but Euliss and Mushet (1999) found that intensive farming reduced numbers of aquatic invertebrate eggs in temporary wetlands.

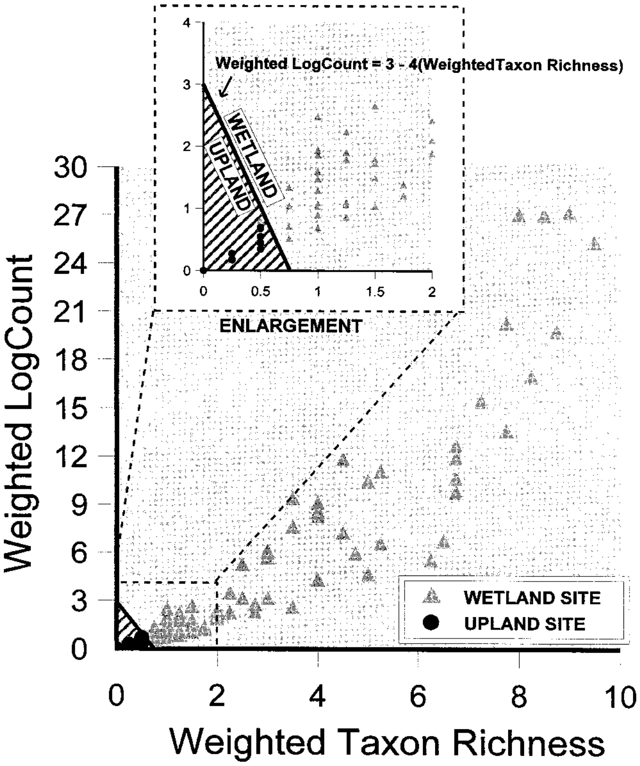

Figure 2. Relationship of LogCount and the number of invertebrate taxa, weighted by habitat affinity, for visually derived field data using compete taxonomy for 62 intensively farmed temporary and seasonal wetlands in the Prairie Pothole Region. Twenty-five upland sites where samples were incorrectly collected from within wetland areas are identified as wetland sites. Thirty upland observations are hidden in the lower, lefthand corner.

Incubation of samples in aquaria failed to separate only 2 sites where obvious depressions existed. Both basins were dry during the 1994 revisit despite the unusually wet conditions throughout the PPR; wetlands adjacent to one of the misclassified sites were fully ponded, whereas the wetlands adjacent to the other dry site that was misclassified were also dry. While not evaluated in our study, sand lenses can provide natural drains in basins. Sand lenses are stringers of sandy material deposited from glacial melting that provide an underground conduit for water flow. Sand lenses are common in glacial till and are known to contribute to differences in ground-water recharge among wetlands (Swanson 1990). The remaining misclassified wetlands had been drained (either by subsurface tile or by shallow ditching), which had not been noted by the field crew when sites initially were sampled. Interestingly, all of these wetlands were classified as wetlands using the field data.

Since definitions of wetlands involve the delineation of distinct cutoff points of variables that occur along gradients (e.g., soils never saturated to soils always saturated, 0% hydrophytes to 100% hydrophytes) (U.S. Army Corps of Engineers 1987), the wetlands most difficult to identify will be those with features falling closest to these cutoff points; in the PPR these are the temporary and seasonal wetlands. Because conventional wetland indicators are of limited value when basins are intensively farmed, aquatic invertebrates may offer the most practical and cost-effective tool to identify farmed wetlands.

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