3-2008

Amphiod Densities and Indices of Wetland Quality Across the Upper-Midwest, USA

Michael J. Anteau
Louisiana State University, Baton Rouge, manteau@usgs.gov

Alan D. Afton
U.S. Geological Survey

AMPHIPOD DENSITIES AND INDICES OF WETLAND QUALITY ACROSS THE UPPER-MIDWEST, USA

Michael J. Anteau[1,2] and Alan D. Afton[3]
[1]*School of Renewable Natural Resources*
Louisiana State University
Baton Rouge, Louisiana, USA 70803

[2]*Present address:*
U.S. Geological Survey
Northern Prairie Wildlife Research Center
Jamestown, North Dakota, USA 58401
E-mail: manteau@usgs.gov

[3]*U.S. Geological Survey*
Louisiana Cooperative Fish and Wildlife Research Unit
Louisiana State University
Baton Rouge, Louisiana, USA 70803

Abstract: Nutritional, behavioral, and diet data for lesser scaup (*Aythya affinis* [Eyton, 1838]) indicates that there has been a decrease in amphipod (*Gammarus lacustris* [G. O. Sars, 1863] and *Hyalella azteca* [Saussure, 1858]) density and wetland quality throughout the upper-Midwest, USA. Accordingly, we estimated densities of *Gammarus* and *Hyalella* in six eco-physiographic regions of Iowa, Minnesota, and North Dakota; 356 randomly selected semipermanent and permanent wetlands were sampled during springs 2004 and 2005. We also examined indices of wetland quality (e.g., turbidity, fish communities, aquatic vegetation) among regions in a random subset of these wetlands (n = 267). *Gammarus* and *Hyalella* were present in 19% and 54% of wetlands sampled, respectively. *Gammarus* and *Hyalella* densities in North Dakota were higher than those in Iowa and Minnesota. Although historical data are limited, our regional mean (1 to 12 m^{-3}) amphipod densities (*Gammarus* + *Hyalella*) were markedly lower than any of the historical density estimates. Fish, important predators of amphipods, occurred in 31%–45% of wetlands in North Dakota, 84% of wetlands in the Red River Valley, and 74%–84% of wetlands in Iowa and Minnesota. Turbidity in wetlands of Minnesota Morainal (4.0 NTU geometric mean) and Red River Valley (6.1 NTU) regions appeared low relative to that of the rest of the upper-Midwest (13.2–17.5 NTU). We conclude that observed estimates of amphipods, fish, and turbidity are consistent with low wetland quality, which has resulted in lower food availability for various wildlife species, especially lesser scaup, which use these wetlands in the upper-Midwest.

Key Words: forage availability, macroinvertebrate, prairie wetlands, scaup, sedimentation, trophic cascade, water quality

INTRODUCTION

Large proportions of wetlands in Iowa, Minnesota, and North Dakota have been drained or otherwise lost in the past 200 years (Dahl 1990), and most remaining wetlands are located in a highly modified landscape, where they are subject to various perturbations (e.g., ditches, drainage tile, sedimentation) that effect their quality. Factors influencing trophic structure and wetland quality have important implications for management of wetlands in the upper-Midwest, USA (Swanson and Nelson 1970, Bouffard and Hanson 1997, Hanson et al. 2005). Semipermanent and permanent wetlands in this landscape naturally undergo marked changes in their biotic and abiotic characteristics as a result of inter-annual climate variations (Euliss et al. 2004). Further, these wetlands may exist in either a clear-water state, dominated by submerged-aquatic vegetation (SAV), or in a turbid state, dominated by phytoplankton (Scheffer et. al 1993, Zimmer et. al 2002). In highly disturbed landscapes, where wetlands are prone to have invasive species present and receive inputs of sediments and nutrients from agricultural activities, wetlands frequently exhibit the turbid state (Hanson et al. 2005).

Although the concept of wetland quality is poorly defined among wetland managers (La Peyre et al. 2001), sediment is the number one pollutant in waters of the United States (U.S. Environmental Protection Agency 1995) and it is an important factor affecting the quality of wetlands (Luo et al. 1997, Gleason et al. 2003). Wetlands with relatively clear water, abundant SAV, and higher macroinvertebrate densities generally provide more food for various wildlife species (Krull 1970, Dieter 1991, Gleason et al. 2003). Therefore, we assume that wetlands with lower sediment influxes and abundant SAV and macroinvertebrates are higher quality, at least from a wildlife habitat perspective.

Amphipods are important indicators of water quality, given their sensitivity to contaminants, pesticides, and pollution (Grue et al. 1988, Covich and Thorp 1991, Tome et al. 1995, Murkin and Ross 2000, Besser et al. 2004). Amphipod densities are positively correlated with SAV (Krull 1970, Anteau 2006, Strayer and Malcom 2007) and negatively correlated with both fish densities (Hanson and Butler 1994, Zimmer et al. 2000, 2001, Anteau 2006) and high levels of suspended sediments (Anteau 2006). Therefore, estimates of amphipod densities across a landscape should index wetland and water quality at a landscape level.

Gammarus lacustris and *Hyalella azteca* (hereafter *Gammarus* and *Hyalella*, respectively) are the most abundant amphipod species in semipermanent and permanent wetlands of the upper-Midwest (Kantrud et al. 1989). Both species are productive, capable of producing multiple broods when the breeding season is relatively long, and often are observed at high densities (thousands m^{-2}; Covich and Thorp 1991, Wen 1992, Pickard and Benke 1996). Amphipods are an important component of secondary production in prairie wetland food webs; they consume detritus and shred coarse particulate organic matter, but also consume epibenthic algae and microbial bacteria (Murkin 1989, Wen 1992, Day et al. 1998, Dvorak et al. 1998, Murkin and Ross 2000).

Amphipods are important prey of fish and wildlife in prairie wetlands and lakes of the upper-Midwest. Species that consume amphipods include fish ranging from fathead minnows (*Pimephales promelas*) to large northern pike (*Esox lucius*; > 50 cm; Peterka 1989, Dvorak et al. 1998, MacNeil et al. 1999), tiger salamanders (*Ambystoma tigrinum*; Olenick and Gee 1981, Kantrud et al. 1989, MacNeil et al. 1999), migrating and breeding diving ducks (*Aythya* spp.), ruddy ducks (*Oxyura jamaicensis*), common goldeneye (*Bucephala clangula*), and several species of dabbling ducks during brood rearing (*Anas* spp.;

Kantrud et al. 1989, Swanson and Duebbert 1989, Krapu and Reinecke 1992, Eadie et al. 1995). Lesser scaup (*Aythya affinis*; hereafter scaup) select for amphipod prey and preferentially forage within wetlands with high amphipod densities, especially during spring migration in the upper-Midwest (Afton et al. 1991, Lindeman and Clark 1999, Anteau and Afton 2006, 2008).

The population decline of scaup over the past 25 years has generated considerable interest in identifying factors negatively affecting these birds (Austin et al. 1998, Afton and Anderson 2001, Anteau and Afton 2004, 2006). Scaup currently are consuming fewer amphipods than did those historically while migrating through the upper-Midwest during spring (Anteau and Afton 2006, 2008). Female scaup migrating throughout the upper-Midwest currently are catabolizing lipids and have fewer lipid reserves than did those historically, likely due to a decline in availability or quality of foods (Anteau and Afton 2004, Anteau et al. 2007). Nutritional and dietary studies of scaup have suggested that there has been a landscape-scale decrease in amphipods on stopover areas in the upper-Midwest (Anteau and Afton 2004, 2006, 2008, Strand 2005). Accordingly, estimating spring amphipod densities in the upper-Midwest was identified as a research priority (Anteau and Afton 2004, 2006).

Other potentially useful biotic and abiotic wetland characteristics that may provide information about water and wetland quality include turbidity, chlorophyll *a*, SAV, fish communities, and specific conductivity. Excessively high turbidity or phytoplankton density (indexed by chlorophyll *a*) may be indicative of agricultural inputs (i.e., sediment and nutrients) or influences of fish communities (Dieter 1991, Scheffer et al. 1993, Hanson et al. 2005). High abundances of SAV often are associated with abundant macroinvertebrate populations (Krull 1970, Anteau 2006). Finally, fish, particularly fathead minnows (*Pimephales promelas*) and common carp (*Cyprinus carpio*), have the potential to decrease macroinvertebrate abundance directly (through predation) and indirectly through trophic cascades (Scheffer et al. 1993, Bouffard and Hanson 1997, Batzer et al. 2000). Abiotic influences of water chemistry may be important indicators of which animal and plant communities are present in wetlands because species have varying tolerances (Kantrud et al. 1989, Peterka 1989). Moreover, there are distinct spatial trends in total dissolved solids and major ion composition based on geologic history across the upper-Midwest (Gorham et al. 1983).

We estimated densities of amphipods throughout the upper-Midwest and evaluated whether there has
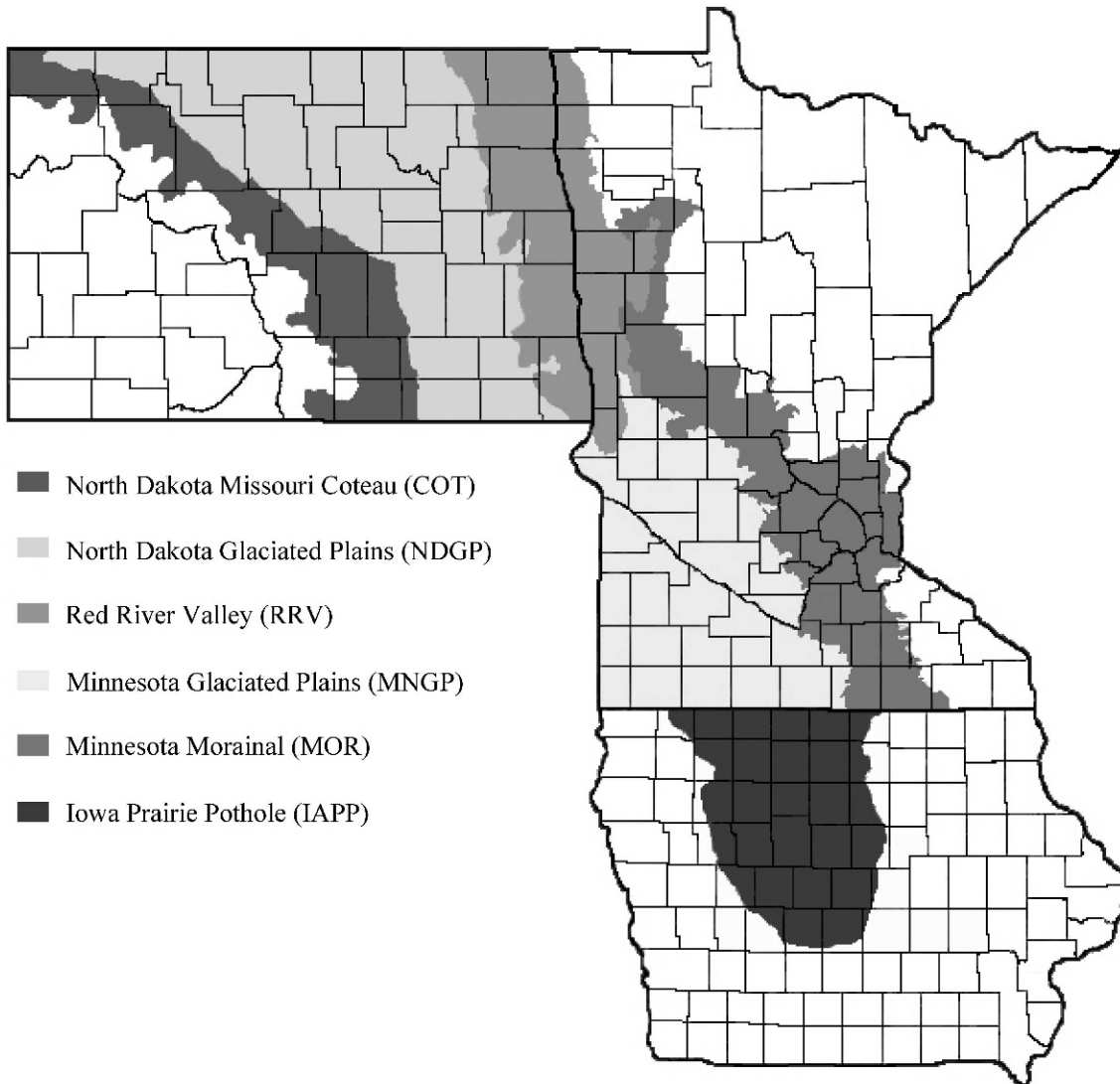
Figure 1.   Map of the study area showing six eco-physiographic regions for wetland sampling (2004–2005) during early spring in the upper-Midwest. Areas in white were not sampled.

been a decline in amphipod densities by comparing current and historical amphipod densities. We also reported other wetland characteristics associated with water and wetland quality and made assessments of wetland quality relative to historical data and regional variations in these indices.

METHODS

Study Area

We sampled semipermanent and permanent wetlands within the Prairie Pothole Region of Iowa, Minnesota, and North Dakota. We stratified the 3-state area into six eco-physiographic regions (hereafter regions) based on watershed and groundwater hydrology, geology, and plant communities (Fig-

ure 1; Kantrud et al. 1989; Minnesota Department of Natural Resources, unpublished data). The Minnesota Glaciated Plains (MNGP) and Minnesota Morainal (MOR) eco-physiographic regions included areas outside the traditional Prairie Pothole Region (Figure 1); however, we included these regions so that results would be relevant to state-specific management and conservation plans.

We used a constrained-random, clustered sampling approach to select wetlands to minimize travel time between wetlands and in areas with few wetlands. We first estimated numbers of townships within each region that had at least 200 ha of semipermanent wetlands (candidate townships for random selection; Table 1), based on converged basin (Johnson and Higgins 1997) or comparable National Wetland Inventory data (see Anteau 2006).

Table 1. Numbers of sampling clusters, wetlands sampled for amphipod density (N_{Amph}), and wetlands sampled for water quality, submerged vegetation, and fish communities ($N_{Complete}$) by region and year, including numbers of candidate townships (T) available for random selection of sampling clusters.

Region	Clusters	N_{Amph}		$N_{Complete}$		T
		2004	2005	2004	2005	
North Dakota Missouri Coteau	3	27	26	9	26	208[a]
North Dakota Glaciated Plains	6	42	50	15	50	364[a]
Red River Valley	3	21	21	11	21	66[a]
Minnesota Morainal	4	28	34	10	34	348[a]
Minnesota Glaciated Plains	4	31	33	18	33	285[a]
Iowa Prairie Pothole	3	20	23	17	23	43[b]
Wetland Total		169	187	80	187	

[a] Townships that contain at least 200 ha of semipermanent wetlands.
[b] Townships that contain at least 200 ha total of semipermanent and permanent wetlands.

In Iowa, we broadened the constraint to include townships with 200 ha of either semipermanent or permanent wetlands. Constraining township selection helped insure that there were enough wetlands to sample within each township.

We allocated numbers of sampling clusters among the six regions (3–6 clusters per region; Table 1) based on region size and numbers of candidate townships available (Table 1, Figure 1). Each region was divided into sub-regions based on latitude, so that there was one sampling cluster per sub-region each year, except in North Dakota Glaciated Plains (NDGP). In NDGP, we assigned two sampling clusters for each sub-region because of the larger width of this region (east to west) relative to other regions (Figure 1).

Each sampling cluster was comprised of three randomly selected 36-square-mile townships (27,972 ha total). The centrums of the second and third townships selected were constrained to be within 50 km of the centrum of the first randomly selected township. We randomly selected three semipermanent or permanent wetlands ($>$ 4 ha) in each township for amphipod and wetland sampling. We randomly selected new townships and wetlands annually within each sub-region from the list of candidate townships to maximize representation of spatial variability in amphipod densities and indices of wetland quality.

We conducted amphipod sampling on 356 wetlands in 2004 and 2005. Wetlands ranged in size from 4 to 6,000 ha; however, 95% of our sample ranged from 4 to 213 ha (based on converged basin or comparable National Wetland Inventory data). Complete wetland surveys (i.e., sampling amphipods, SAV, fish communities, and water quality [see following]) were conducted on a random subset of the wetlands surveyed for amphipod densities in 2004 and on all wetlands in 2005; thus we conducted complete surveys on 267 wetlands (Table 1).

Wetland Sampling

We timed wetland sampling to coincide with the estimated middle of the scaup migration period, when relatively large numbers of migrating scaup were present on our study area (see Anteau 2006); thus, we started sampling in the southern portion of the study area and worked north. This approach ensured that our estimates of amphipod densities were representative for that available to scaup during spring migration and our sampling occurred at similar times relative to phenology each spring. Sampling was conducted from April 3 to May 16, 2004 and from March 30 to May 3, 2005, well before the season's first recruits of amphipods are observed (mid to late June; Wen 1992).

Amphipod Density. We drew four transects on a map of each wetland by randomly selecting four bearings (0 to 359); transects radiated out from the center to the bank of the wetland. Each transect had two sampling stations; the first station was 10 m past the inner ring of the emergent vegetation and the second was 50 m away from the first station along the transect (toward the center). However, we limited station locations to depths between 0.5 and 3 m for ease of sampling and because these are depths that scaup feed in spring (Austin et al. 1998). Thus, in few instances ($<$ 5% of transects), station locations were adjusted along transects to accommodate depth requirements.

At each station, we recorded water depth and sampled amphipod density with a D-shaped-sweep net (1,200 μm mesh, 0.072 m^2 opening, WARD's Natural Science, Rochester, New York). Each amphipod sample consisted of a bottom sweep

(skimming the net along the bottom for a distance equal to the depth at the sampling station) and an upward sweep through the water column. This pattern ensured equal representation of bottom and water column in each sample. When SAV or other debris was brought up with the sweep-net, it was included in the sample, unless greater than 50% of the object hung outside the net. Although SAV was present (see Results), it was never so dense that it impaired our ability to effectively sample amphipods with sweep-nets. In the field, sweep-net samples (n = 8 per wetland) were combined into a single composite sample per wetland, preserved in a 95% ethanol solution, and then transported to the laboratory for processing.

In the laboratory, each composite sample was stained with Rose Bengal (Sigma # R3877, Sigma-Aldrich Corp., St. Louis, Missouri), sieved (500 μm mesh), floated with sugar and water solution in a large dissecting tray, and all plant and benthic material was searched. We sorted and counted all amphipods using a lighted magnifying glass and a stereomicroscope.

We calculated the total water volume swept (VS; m^3) for each wetland with the equation:

$$VS = 2\left(\sum D_i\right) \times SN$$

where D_i = depth (m) at each sampling station, and SN = sweep-net opening ($0.072\ m^2$). We calculated densities (individuals per m^3; hereafter m^{-3}) of each species of amphipod for each wetland by dividing the count of each species by VS. Because many of the historical studies reported amphipod densities by unit area of water surface, we also estimated the number of amphipods per m^2 of water surface for each wetland by multiplying the density (m^{-3}) to the average depth of all sampling stations.

Estimation of Submerged Aquatic Vegetation. We sampled SAV for each station after amphipod sampling was complete to avoid disturbing the distribution of amphipods. We used grab sampling to estimate relative abundance of SAV along a sub-transect starting at each sampling station and running parallel to the bank. Each sub-transect had 10 grabs (1/meter) using a 36-tine Lake Rake (Ben Meadows Co., Janesville, Wisconsin) gently dug into the bottom and pulled straight up (Nyman and Chabreck 1996). For each grab, presence/absence of vegetation (rhizomes and shoots were included) was recorded. Relative abundance was estimated for each wetland by the proportion of grabs with SAV present (n/80).

Estimation of Fish Abundance. We indexed abundance of various fish species with an experimental gill net (21×2 m with $7 - 3$ m panels ranging in mesh size from 1.9–7.6 cm) set on a fifth transect. The end of the net with the smaller mesh sized panels was set about 10 m from the open water-emergent vegetation interface and extended along the transect toward the center of the wetland. We also set five minnow traps (Gee style; 44 cm long, 23 cm diameter cylinder with 22 mm-inward-funnel openings on both ends and made of 6.4 mm galvanized mesh) on each wetland to supplement data from the gill net; one minnow trap per transect was placed at the transition between emergent vegetation and open water. Gill nets and minnow traps were set and retrieved for the same time period within each wetland, 14 to 24 hours (85% of sets were over 18 hours), always including an overnight sampling period.

Fish caught in all five traps and in the gill net were enumerated by species. We subsequently classified fish species into one of four categories: 1) fathead minnows, 2) large Cypriniformes (carp, buffalo [*Ictiobus* sp.], and suckers [*Catostomus* sp.]), 3) small fish (other minnows [Cyprinidae], darters [Anhingidae], sticklebacks [Gasterosteidae], and mudminnows [*Umbra* sp.]), and 4) other large fish (e.g., northern pike, walleye [*Sander vitreus*], perch [*Perca* sp.], sunfish [*Lepomis* spp.], bullhead and catfish [Ictaluridae]). All fathead minnows and small fish were caught with minnow traps and all large Cypriniformes and most large fish were caught in gill nets; however, occasionally small sunfish, perch, or bullhead were caught in minnow traps and were pooled with the sample of those caught in gill nets. We calculated catch per unit effort (relative abundances) by dividing total numbers of each fish in each class by the hours that the gill net and five minnow traps were in the water.

Water Quality. We measured turbidity ($\pm$ 1 nephelometric turbidity unit [NTU]), chlorophyll *a* ($\pm$ 1 μg/l), and specific conductance ($\pm$ 1 μS/cm) with portable water quality meters (YSI 6600 sonde with optical chlorophyll [YSI 6025] and turbidity [YSI 6136] probes; YSI Inc. Yellow Springs, Ohio) at the first four transects near the center of the wetland. All measurements were averaged for each wetland.

Statistical Analyses

We compared densities (m^{-2} and m^{-3}) of *Gammarus* and *Hyalella* separately among regions and between years with analyses of variance (PROC MIXED; SAS Institute 2002). *Gammarus* and *Hyalella* densities where $\log_e$ (+1) transformed to meet assumptions of normality (Devore 2000); we report back-transformed geometric means. For each
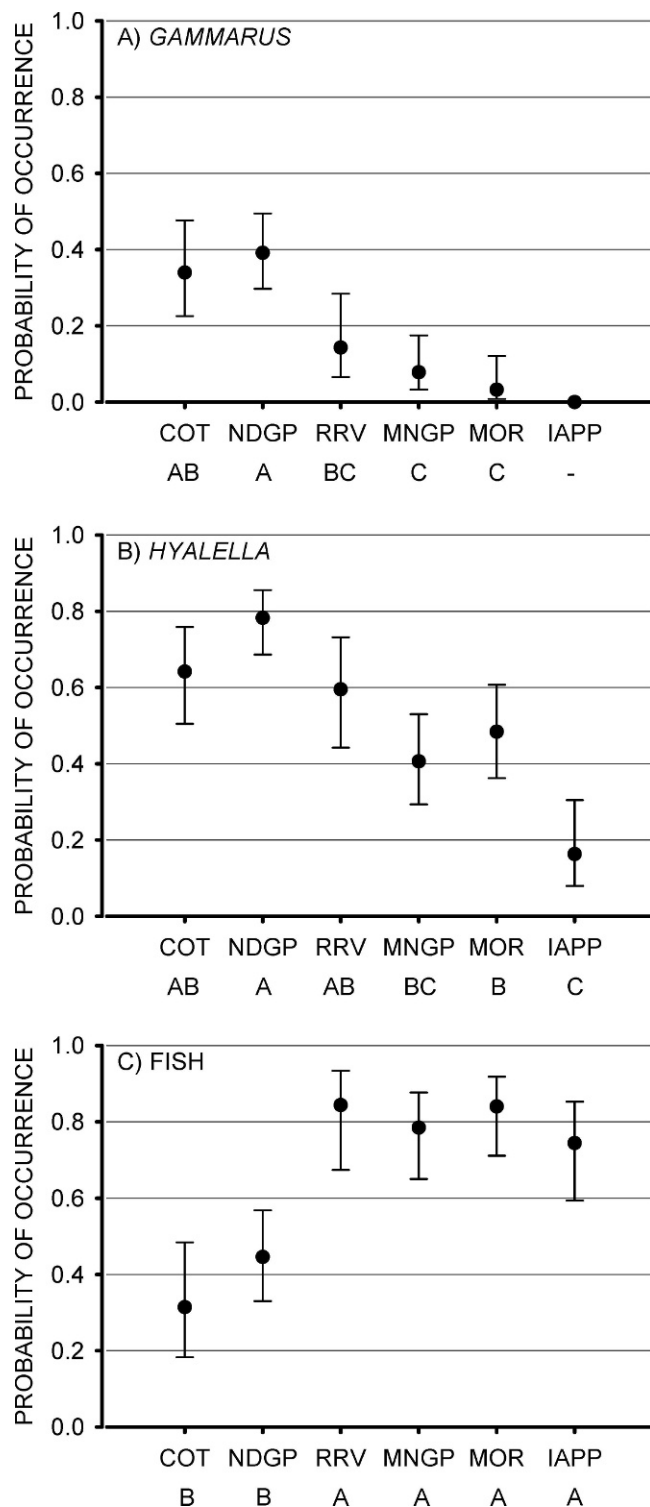
Figure 2.   Probability of occurrence ($\pm$ 95% CI) of A) *Gammarus lacustris*, B) *Hyalella azteca*, and C) fish by regions in the upper-Midwest, springs 2004 and 2005 combined. Regions depicted as: COT = ND Missouri Coteau, NDGP = ND Glaciated Plains, RRV = Red River Valley of MN and ND, MNGP = MN Glaciated Plains, MOR = MN Morainal, and IAPP = IA Prairie Pothole. Capital letters beneath region labels are Tukey-Kramer adjusted mean grouping at P < 0.05.

final model, we used the PDMIX800 macro (Saxton 1998) to get Tukey-Kramer adjusted mean letter groupings for each region. We compared the probability of occurrence for *Gammarus*, *Hyalella*, and fish (all species combined) among regions with separate logistic regressions (PROC GLIMMIX). In these three models, we specified region as the class variable, using a binomial distribution and a logit link function. We used the LSMEANS statement to calculate least squares mean probabilities of occurrence with 95% confidence intervals (CI), and the PDIFF option to conduct contrasts among regions and calculate Tukey-Kramer adjusted mean letter groupings for each region (SAS Institute 2002). We did not include data from the Iowa Prairie Pothole region (IAPP) in the *Gammarus* model because no *Gammarus* were found there.

We compared indices of wetland quality (SAV, specific conductance, chlorophyll *a*, turbidity, fathead minnows, large Cypriniformes, large fish, and small fish) among regions and between years with a multivariate analysis of variance (MANOVA, PROC GLM; SAS Institute 2002). Year was not significant in the initial model ($P > 0.05$) and, thus was excluded. We then conducted contrasts to examine regional differences in all responses using Tukey-Kramer adjusted least-squares-mean groupings (pdiff-all option; $\alpha = 0.05$; PROC GLM; SAS Institute 2002).

RESULTS

Amphipod Densities

Gammarus and *Hyalella* were present in 19% and 54% of all wetlands surveyed, respectively; *Gammarus* and *Hyalella* densities ranged from 0–1,147 and 0–1,507 m^{-3}, respectively. Densities of *Gammarus* and *Hyalella* followed a highly right-skewed distribution, and were less than or equal to 5 m^{-3} in 92 and 61% of wetlands, respectively. *Gammarus* occurred most frequently in wetlands of the Missouri Coteau of North Dakota (COT) and NDGP, and less so in other regions (Minnesota Glaciated Plains [MNGP] and Minnesota Morainal [MOR]). *Hyalella* occurred most frequently in the COT, NDGP, and Red River Valley (RRV) and less so in other regions (Figure 2). *Gammarus* were not found in wetlands of the IAPP and probability of occurrence of *Hyalella* also was low in wetlands of this region (Figure 2).

Gammarus and *Hyalella* densities differed among regions ($F_{5,350} = 9.27$, P < 0.001 and $F_{5,349} = 9.83$, P < 0.001, respectively; Figure 3). *Gammarus* densities did not vary annually (P > 0.05), so year
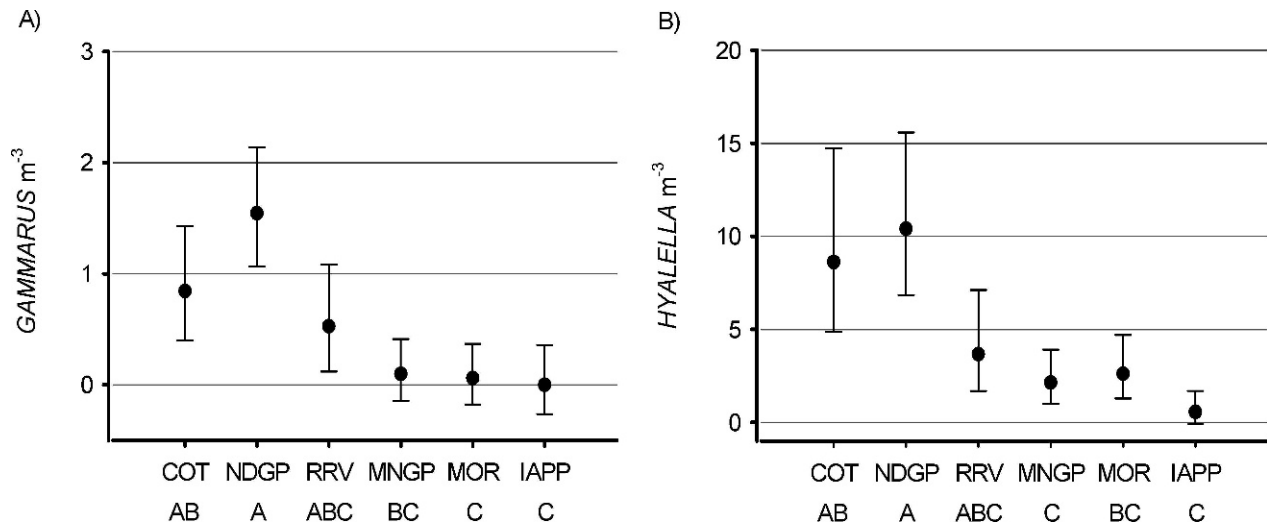
Figure 3. Geometric least-squares mean densities ($\pm$ 95% CI) of A) *Gammarus lacustris* and B) *Hyalella azteca* by regions in the upper-Midwest, springs 2004 and 2005 combined. Regions depicted as: COT = ND Missouri Coteau, NDGP = ND Glaciated Plains, RRV = Red River Valley of MN and ND, MNGP = MN Glaciated Plains, MOR = MN Morainal, and IAPP = IA Prairie Pothole. Capital letters beneath region labels are Tukey-Kramer adjusted mean grouping at P < 0.05.

was removed from the model. However, overall *Hyalella* density was 3 m^{-3} higher in 2005 than in 2004 ($F_{1,349}$ = 13.11, P < 0.001). *Hyalella* generally were more abundant than were *Gammarus* in all regions (Figure 3). *Gammarus* and *Hyalella* densities were higher in NDGP than MOR, MNGP, and IAPP, whereas densities in RRV were intermediate between these two groups of regions (Figure 3). *Gammarus* density was higher in COT than that in MOR or IAPP (Figure 3). *Hyalella* density also was higher in COT than in MNGP and IAPP (Figure 3). Overall densities, by volume, of *Gammarus* and *Hyalella* combined were 12, 9, 4, 3, 2, and 1 m^{-3} for NDGP, COT, RRV, MOR, MNGP, and IAPP, respectively (see Figure 3). Overall densities, by area, of *Gammarus* and *Hyalella* combined were 14, 10, 5, 3, 2, and 1 m^{-2} for NDGP, COT, RRV, MOR, MNGP, and IAPP, respectively.

Wetland Quality

Wetland characteristics also varied by region ($F_{8,258}$ = 9.54, P < 0.001). Partial correlation coefficients from the MANOVA indicated: 1) the abundance of SAV in wetlands was negatively correlated with turbidity (r = −0.485, P < 0.001), chlorophyll a (r = −0.316, P < 0.001), specific conductance (r = −0.162, P = 0.008), and abundances of fathead minnows (r = −0.216, P < 0.001), large Cypriniformes (r = −0.234, P < 0.001), and large fish (r = −0.177, P = 0.004); 2) the level of turbidity in wetlands was positively correlated with abundances of fathead minnows (r = 0.162, P = 0.009) and large

Cypriniformes (r = 0.188, P = 0.002), specific conductance (r = 0.176, P = 0.004), and chlorophyll a (r = 0.620, P < 0.001); 3) specific conductance was not correlated with abundances of any of our fish classes (Ps > 0.175); and 4) the level of chlorophyll a was positively correlated with the abundances of fathead minnows (r = 0.168, P = 0.006) and large Cypriniformes (r = 0.185, P = 0.003).

Specific conductance was markedly higher in COT and NDGP than in RRV, MNGP, MOR, and IAPP (Figure 4). Turbidity was higher in IAPP, COT, NDGP, and MNGP than in RRV and MOR (Figure 4). Chlorophyll a was nearly two times higher in IAPP than any other region, but was significantly different (after Tukey-Kramer adjustments) from only RRV and MOR (Figure 4). SAV was lower in IAPP than that in MOR and RRV (Figure 4).

Regional probabilities of fish occurrences ranged from 0.31–0.84, and fish occurred in wetlands of RRV, MNGP, MOR, and IAPP more frequently than those of COT and NDGP (Figure 2). Fathead minnows were more abundant in wetlands of MNGP and NDGP than in those of COT and IAPP (Figure 5). Large Cypriniformes were more abundant in wetlands of IAPP than in those of any other region (Figure 5). Small fish were more abundant in wetlands of MOR than in those of IAPP, COT, and NDGP (Figure 5). Large fish were more abundant in wetlands of MNGP, MOR, and IAPP than in those of COT and NDGP; they were intermediate in RRV (Figure 5).
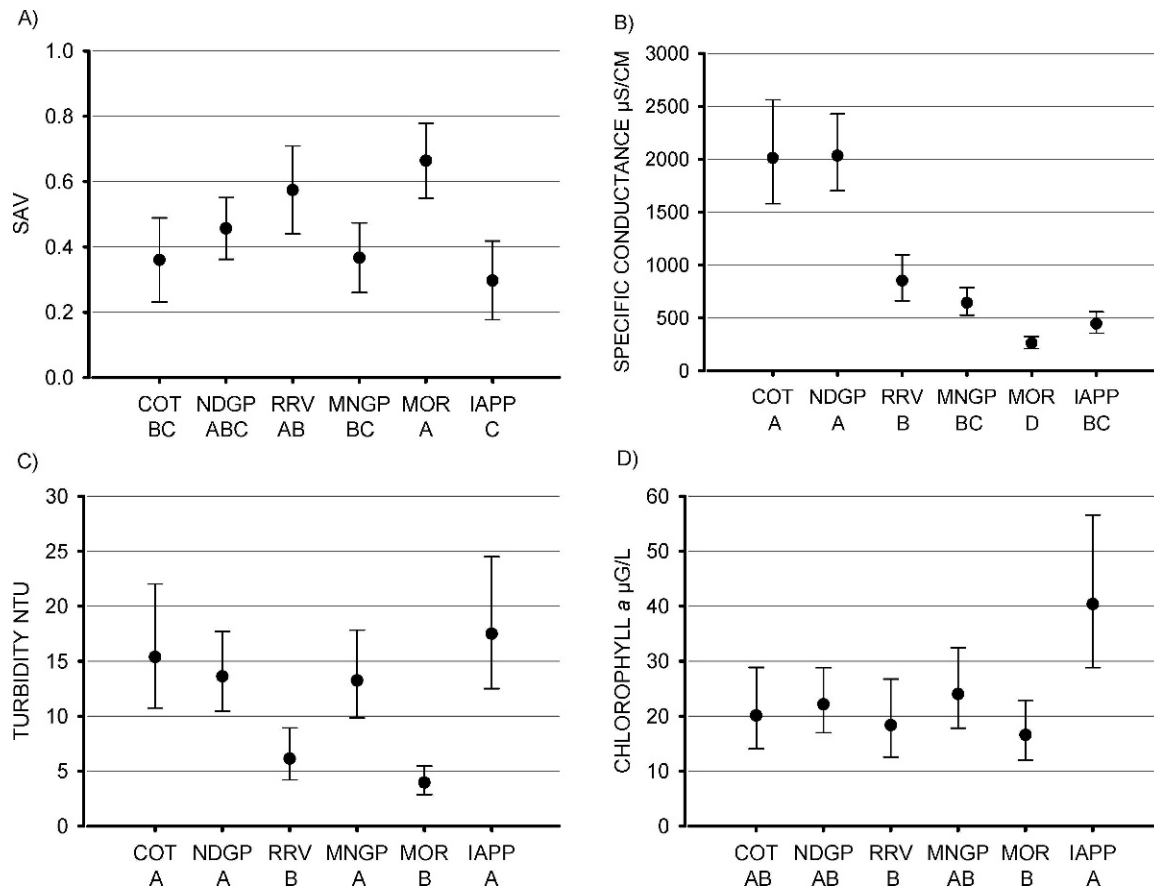
Figure 4.   Geometric least-squares means (± 95% CI) of relative abundance of A) submerged aquatic vegetation (SAV), B) specific conductance, C) turbidity, and D) chlorophyll *a* by regions in the upper-Midwest, springs 2004 and 2005 combined. Regions depicted as: COT = ND Missouri Coteau, NDGP = ND Glaciated Plains, RRV = Red River Valley of MN and ND, MNGP = MN Glaciated Plains, MOR = MN Morainal, and IAPP = IA Prairie Pothole. Capital letters beneath region labels are Tukey-Kramer adjusted mean grouping at P < 0.05.

DISCUSSION

Amphipod Densities

Comparable historical estimates of spring amphipod densities are limited across our study area. However, two historical data sets are available within RRV of Minnesota and NDGP as are others from the Canadian portion of the Prairie Pothole Region. In 1961, *Gammarus* densities were 548 m^{-2} at Warren Lake, Minnesota (RRV), based on a report of 34 g (wet mass) m^{-2} of *Gammarus* (Bartonek and Murdy 1970) and an 0.062 g average wet mass of *Gammarus* (D. M. Mushet, U.S. Geological Survey, unpublished data). In the late 1980s, *Gammarus* and *Hyalella* densities averaged 53 and 41 m^{-2}, respectively for four bays within the Devil's Lake Chain, North Dakota (NDGP; Brooks 1989). In contrast, the bay of the Devil's Lake Chain that we sampled in 2005, only had 7 and 3 m^{-2} of each species, respectively. Studies conducted in southwestern Manitoba in the late 1970s reported average

Gammarus densities of 163 m^{-3} for three wetlands (Salki 1981) and geometric mean *Gammarus* and *Hyalella* densities of 71 and 28 m^{-3}, respectively, for 19 wetlands (Afton and Hier 1991). In the late 1980s, *Hyalella* densities ranged between 1,000 and 2,000 m^{-2} in southern Alberta (Wen 1992). All of the reported historical values occurred prior to mid to late June, and thus probably before the first cohort of amphipods likely was produced (Wen 1992), except for data from the RRV that was collected in summer. Wetlands might not have been randomly selected in some of the historical studies, which may have biased estimates. However, our observed regional mean densities of amphipods were very low relative to all available historical densities. Similarly, amphipod densities collected in mid-August from 2000 to 2007 at Thief Lake Wildlife Management Area in northwestern Minnesota were 94% lower than those observed at the same time of year in the 1980s (J. Huener, Minnesota Department of Natural Resources, unpublished data). We did not
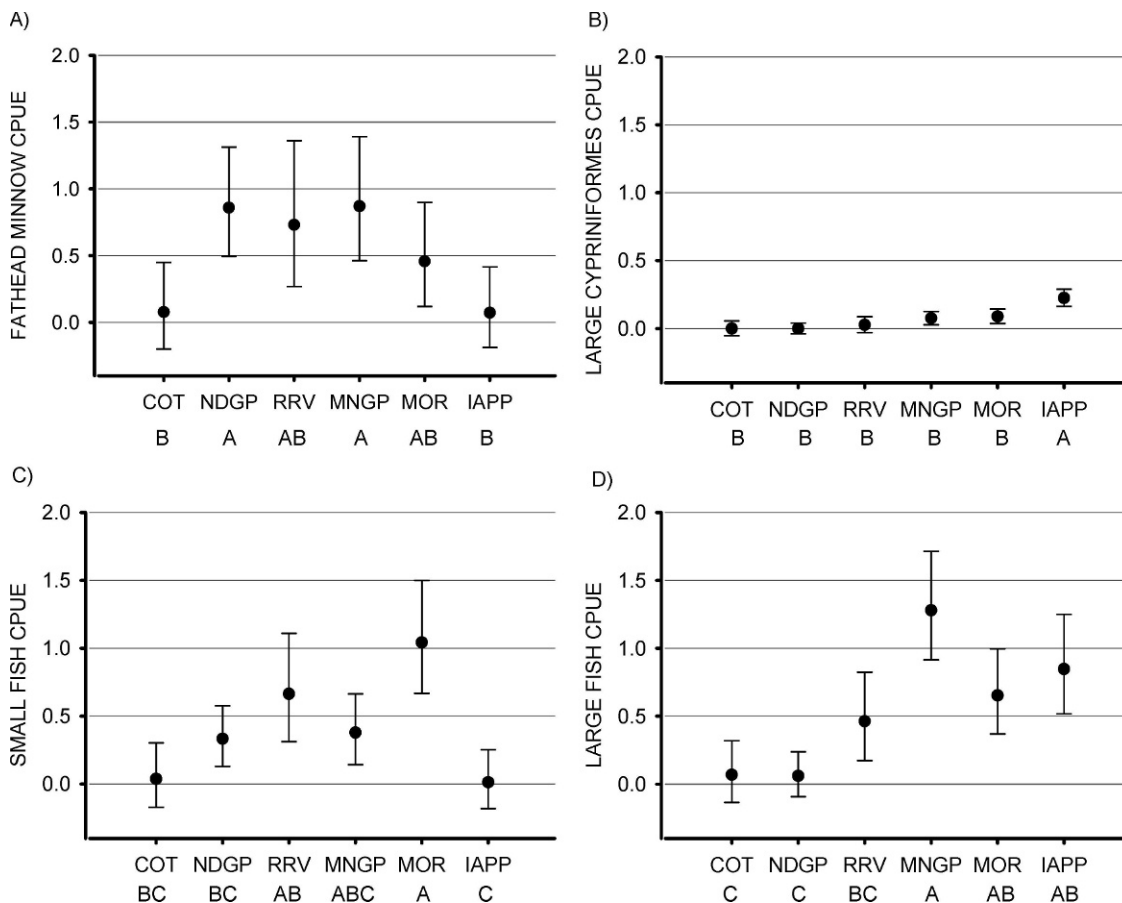
Figure 5.   Geometric least-squares mean catch per unit effort (CPUE; ± 95% CI) of A) fathead minnows, B) large Cypriniformes, C) small fish, and D) large fish by regions in the upper-Midwest, springs 2004 and 2005 combined. Regions depicted as: COT = ND Missouri Coteau, NDGP = ND Glaciated Plains, RRV = Red River Valley of MN and ND, MNGP = MN Glaciated Plains, MOR = MN Morainal, and IAPP = IA Prairie Pothole. Capital letters beneath region labels are Tukey-Kramer adjusted mean grouping at P < 0.05.

detect *Gammarus* in wetlands sampled in IAPP and their occurrence and density were low in MNGP and MOR (Figures 2 and 3). Historical accounts of diving-duck use and descriptions of wetlands in IAPP (Low 1941) suggest that *Gammarus* probably occurred there historically. Densities of amphipods in most wetlands across the upper-Midwest landscape are low relative to potential densities because we observed amphipod densities in very few wetlands that were as high as those reported in historical studies. Female scaup migrating through Iowa, Minnesota, and North Dakota in 2004 and 2005 were catabolizing lipid reserves and had low lipid reserves levels in relation to historical data (Anteau and Afton 2004, Anteau 2006). Several lines of evidence indicate that scaup strongly prefer amphipods as food during spring migration in the upper-Midwest (Rogers and Korschgen 1966, Bartonek and Hickey 1969, Swanson and Nelson 1970, Swanson and Duebbert 1989, Afton and Hier 1991, Afton et al. 1991, Lindeman and Clark 1999, Strand

2005, Anteau 2006). However, overall food consumption and particularly amphipod consumption by scaup across the upper-Midwest currently is low relative to data from the 1980s (Anteau and Afton 2006, 2008). Further, consumption of amphipods by scaup during spring and early summer throughout the Prairie Pothole Region in the 1960s was higher than in the 1980s (Rogers and Korschgen 1966, Bartonek and Hickey 1969, Swanson and Nelson 1970, Swanson and Duebbert 1989, Afton and Hier 1991, Afton et al. 1991). We previously speculated that availability of foods, primarily amphipods, have declined for scaup in the upper-Midwest (Anteau and Afton 2004, 2006), and our estimates presented here for *Gammarus* and *Hyalella* densities across this large landscape are consistent with this hypothesis.

Spring amphipod densities primarily are influenced by winter survival and breeding productivity in the previous year because the first annual breeding period for amphipods is late June to early July (Wen 1992). Amphipods over winter as adults in prairie wetlands,

and high survival is required for them to be abundant in early spring (Arts et al. 1995, Lindeman and Clark 1999, MacNeil et al. 1999). Amphipods are susceptible to fish predation year around, unlike many other invertebrates that are more seasonally available (MacNeil et al. 1999). Thus, over-winter survival of amphipods may be a major source of annual variation in amphipod densities. However, we did not detect annual variation in *Gammarus* densities despite observations of widespread winterkills of fish throughout MNGP and MOR in 2004 and few isolated winterkills observed there in 2005. *Hyalella* density was slightly higher in spring 2005 than in spring 2004, perhaps due to winterkill conditions in 2003–2004 either causing winterkills of *Hyalella*, or through the reduction of fish abundance allowing for better amphipod recruitment and survival in the following year. However, annual variation in *Hyalella* densities were relatively small in relation to that observed among regions and the range of observed densities among wetlands (see Figure 3).

We observed a general northwest to southeast cline in amphipod densities and specific conductance (Figures 3, 4), but we caution interpreting this apparent correlation because it is based on regional means and not a formal analysis where the wetland is the experimental unit. It is perhaps noteworthy that the percentage of wetlands that have been drained and intensity of agriculture also generally follows a southeast to northwest cline (Galatowitsch and van der Valk 1994). Hanson et al. (2005) concluded that biotic factors were stronger predictors of ecosystem structure than abiotic factors. Similarly, Anteau (2006) found that specific conductance was not correlated with amphipod densities; rather amphipod densities were positively correlated with SAV and negatively correlated with abundance of fish and indicators of sedimentation into wetlands. Therefore, the northwest to southeast clines in amphipod densities may be coincidental to that observed for specific conductance or are indirectly correlated through other responses (e.g., fish presence, surface-water connectivity).

Wetland Quality

Fish Communities.   A total of 89%, 42%, and 49% of wetlands in Iowa, Minnesota, and North Dakota, respectively, were drained or otherwise lost prior to 1980 (Dahl 1990). The process of wetland drainage has increased the connectivity of remaining wetlands and provided higher and more stable water regimes through increased drainage tile, ditches, and culverts that facilitate colonization and over-winter survival of fish into historically fishless wetlands (Zimmer et

al. 2000, 2001, Hanson et al. 2005). Moreover, connectivity of wetlands and the survivability of fish may have increased during the long, persistent wet cycle of the 1990s (Hanson et al. 2005). However, this wet cycle ended in the early 2000s (U.S. Fish and Wildlife Service 2005).

Historically, only about 10%–20% of deep northern prairie wetlands (1–5 m deep) supported over-wintering fish communities (Peterka 1989). Several studies speculated that natural invasions or introductions of fish have increased recently in semipermanent and permanent wetlands in the upper-Midwest (Hanson and Riggs 1995, Bouffard and Hanson 1997, Zimmer et al. 2002). Our data support this idea; we found frequent occurrences of fish throughout the upper-Midwest, especially in Minnesota and Iowa (Figure 2), indicating an increase in fish occurrence from those reported historically.

Fish can reduce abundance, biomass, activity, and size of amphipods and other macroinvertebrates directly through predation and indirectly by altering the trophic structure of wetlands (Wellborn 1994, Hanson and Riggs 1995, Bouffard and Hanson 1997, Duffy 1998, Wooster 1998, Batzer et al. 2000, Zimmer et al. 2001, 2002, Hanson et al. 2005). Although mechanisms are poorly understood, fathead minnows and carp can increase wetland turbidity, which may decrease SAV and macroinvertebrates, including amphipods (Hanson and Butler 1994, Zimmer et. al 2001, 2002). Our data are consistent with these postulated mechanisms; fathead minnow and large Cypriniformes abundances were positively correlated with turbidity and chlorophyll *a* and negatively correlated with abundance of SAV in wetlands. Accordingly, the increase of fish occurrence in wetlands across the upper-Midwest probably has decreased wetland quality.

Turbidity and Chlorophyll a. Measurements of turbidity in early spring probably provide a good index of mineral sedimentation in wetlands because sedimentation rates typically are highest during spring run-off (Dieter 1991, Gleason and Euliss 1998). However, the amount of phytoplankton (chlorophyll *a*) also is a component of turbidity; chlorophyll *a* can be influenced by nutrient run-off, fish abundance, or the amount of decomposing vegetation in spring (Wen 1992, Hanson and Butler 1994). Fish can increase turbidity directly by stirring sediments (Bouffard and Hanson 1997). Particle size of sediments within a given region also may influence movement into wetlands and the duration of suspension in the water column (Tanner and Jackson 1947).

Agriculture and other anthropogenic influences accelerate wind and water facilitated erosion of soils, and thus affect sedimentation into prairie wetlands,

especially during high spring run-off over bare fields (Martin and Hartman 1987, Dieter 1991, Gleason and Euliss 1998). Sedimentation may proceed slowly or can fill wetlands in a single catastrophic event (Gleason and Euliss 1998). Sediments settling in wetlands reduce depth, thereby altering hydrologic character (Luo et al. 1997) and community composition of wetlands. These factors affect plants that have specific depth tolerances (Gleason and Euliss 1998) or animals that must over-winter in wetlands (e.g., amphipods; Arts et al. 1995). Suspended sediment and phytoplankton can reduce light penetration and limit SAV and associated invertebrate abundances (Dieter 1991, Gleason and Euliss 1998). The observed negative correlations of turbidity and chlorophyll *a* with SAV are consistent with such relationships.

Sedimentation may provide conditions favorable for monotypic stands of cattail (*Typha* spp.) that reduce open-water zones of wetlands (Gleason and Euliss 1998, Gleason et al. 2003). Cattail historically was rare in northern prairie wetlands (Kantrud 1992), but cattail-choked semipermanent or permanent wetlands currently are widespread in parts of Iowa, Minnesota, and North Dakota (Kantrud 1992; M. J. Anteau, unpublished data).

Turbidity levels averaged 3.8 NTU (arithmetic mean; range 0.3–31.0 NTU) in a large sample of fishless and non-agriculturally impacted boreal wetlands in north-central Alberta (Bayley and Prather 2003). In wetlands of MOR, turbidity was similar to that in north-central Alberta. However, wetlands in all other study regions generally had much higher turbidity (Figure 4; range 1–297 NTU), which may indicate high levels of sedimentation or fish influence in these regions. In COT and NDGP, sedimentation into wetlands may be relatively high because relative levels of turbidity were high, but fish occurrences were low and chlorophyll *a* levels were not elevated (relative to other regions). In IAPP, turbidity and chlorophyll *a* levels of wetlands were very high; however, carp were abundant, complicating interpretations. The myriad of factors that can elevate turbidity and phytoplankton levels in wetlands of the upper-Midwest clearly deserve additional study, especially because problems appear widespread within this large landscape.

Submerged Aquatic Vegetation. Reductions in SAV frequently are correlated with declines in invertebrate densities or biomass (Krull 1970, Euliss and Grodhaus 1987, Neill and Cornwell 1992, Schriver et al. 1995, Gleason and Euliss 1998). Moreover, loss of vegetative structure and complexity in wetlands also increase susceptibility of macroinvertebrates to fish predation (MacNeil et al. 1999). Wetlands of MOR

and RRV had the highest SAV and the lowest turbidity levels. We sampled vegetation during spring; thus, some species of SAV that mature later in the season might be underrepresented, potentially biasing our results. Moreover, we did not quantify vegetation by species, and different species of SAV support different densities of macroinvertebrates (Krull 1970).

Conclusions

Our estimates of *Gammarus* and *Hyalella* densities are consistent with the hypothesis that amphipod densities in the upper-Midwest are in decline. Additionally, our results are consistent with previous findings that fish are becoming more common in wetlands throughout the area (Hanson and Riggs 1995, Bouffard and Hanson 1997, Zimmer et al. 2002). Turbidity levels of wetlands generally were high across most of the upper-Midwest, which may indicate problems with sedimentation into wetlands, especially in North Dakota. Accordingly, our regional measurements of turbidity, and amphipod and fish abundance are consistent with landscape-wide declines in wetland quality in the upper-Midwest. Efforts to slow degradation of wetlands by reducing sedimentation and fish introductions, and restoring natural hydrology and isolation of wetlands connected by drainage activities, could improve wetland quality in the upper-Midwest. For conservation efforts to be most effective, several research and conservation issues should be addressed including: 1) establishing a clear definition of wetland quality with standard metrics to facilitate evaluation and assessment of conservation activities; 2) examining specific factors affecting turbidity levels in wetlands (e.g., sedimentation, fish communities, eutrophication, partial size); and 3) identifying factors regulating amphipod and fish abundance in wetlands.

LITERATURE CITED

Afton, A. D. and M. G. Anderson. 2001. Declining scaup populations: a retrospective analysis of long-term population and harvest survey data. Journal of Wildlife Management 65:781–96.

Afton, A. D. and R. H. Hier. 1991. Diets of lesser scaup breeding in Manitoba. Journal of Field Ornithology 62:325–34.

Afton, A. D., R. H. Hier, and S. L. Paulus. 1991. Scaup diets during migration and winter in the Mississippi Flyway. Canadian Journal of Zoology 69:328–33.

Anteau, M. J. 2006. Ecology of lesser scaup and amphipods in the upper-Midwest: scope and mechanisms of the Spring Condition Hypothesis and implications for migration habitat conservation. Ph.D. Dissertation. Louisiana State University, Baton Rouge, LA, USA.<http://etd.lsu.edu/docs/available/etd-01242006-093828>.

Anteau, M. J. and A. D. Afton. 2004. Nutrient reserves of lesser scaup during spring migration in the Mississippi Flyway: a test of the Spring Condition Hypothesis. Auk 121:917–29.

Anteau, M. J. and A. D. Afton. 2006. Diet shifts of lesser scaup are consistent with the spring condition hypothesis. Canadian Journal of Zoology 86:779–86.

Anteau, M. J. and A. D. Afton. 2008. Diets of lesser scaup during spring migration throughout the upper-Midwest are consistent with the Spring Condition Hypothesis. Waterbirds: In press.

Anteau, M. J., A. D. Afton, C. M. Custer, and T. W. Custer. 2007. Influences of cadmium, mercury, and selenium on nutrient reserves of female lesser scaup during winter and spring migration. Environmental Toxicology and Chemistry 26:515–20.

Arts, M. T., M. E. Ferguson, N. E. Glozier, R. D. Robarts, and D. B. Donald. 1995. Spatial and temporal variability in lipid dynamics of common amphipods: assessing the potential for uptake of lipophilic contaminants. Ecotoxicology 4:91–113.

Austin, J. E., C. M. Custer, and A. D. Afton. 1998. Lesser scaup (*Aythya affinis*). The Birds of North America, Number 338. The American Ornithologists' Union, Washington, DC, USA. and the Academy of Natural Sciences, Philadelphia, PA, USA.

Bartonek, J. C. and J. J. Hickey. 1969. Food habits of canvasbacks, redheads, and lesser scaup in Manitoba. Condor 71:280–90.

Bartonek, J. C. and H. W. Murdy. 1970. Summer foods of lesser scaup in subarctic taiga. Arctic 23:35–44.

Batzer, D. P., C. R. Pusateri, and R. Vetter. 2000. Impacts of fish predation on marsh invertebrates: direct and indirect effects. Wetlands 20:307–12.

Bayley, S. E. and C. M. Prather. 2003. Do wetland lakes exhibit alternative stable states? submersed aquatic vegetation and chlorophyll in western boreal shallow lakes. Limnology and Oceanography 48:2335–45.

Besser, J. M., W. G. Brumbaugh, N. E. Kemble, T. W. May, and C. G. Ingersoil. 2004. Effects of sediment characteristics on the toxicity of chromium (III) and Chromium (IV) to the amphipod *Hyalella azteca*. Environmental Science and Technology 38:6210–16.

Bouffard, S. H. and M. A. Hanson. 1997. Fish in waterfowl marshes: waterfowl managers' perspective. Wildlife Society Bulletin 25:146–57.

Brooks, J. J., Jr. 1989. Distribution and relative abundance of *Gammarus lacustris* and *Hyalella azteca* in the Devils Lake Chain, North Dakota. M.S. Thesis. North Dakota State University, Fargo, North Dakota, USA.

Covich, A. P. and J. H. Thorp. 1991. Crustacea: introduction and peracarida. p. 665–89. *In* J. H. Thorp and A. P. Covich (eds.) Ecology and Classifications of North American Freshwater Invertebrates. Academic Press, San Diego, CA, USA.

Dahl, T. E. 1990. Wetland loss in the United States, 1780's to 1980's. U.S. Fish and Wildlife Service, Washington, DC, USA.

Day, J. W., Jr., E. Pieczynska, and B. Ulehlova. 1998. Further fate of organic matter in wetlands. p. 169–91. *In* D. F. Westlate, J. Kvet, and A. Szczepanski (eds.) The Production Ecology of Wetlands. Cambridge University Press, New York, NY, USA.

Devore, J. L. 2000. Probability and Statistics for Engineering and the Sciences. Duxbury, Pacific Grove, CA, USA.

Dieter, C. D. 1991. Water turbidity in tilled and untilled prairie wetlands. Journal of Freshwater Ecology 6:185–89.

Duffy, W. G. 1998. Population dynamics, production, and prey consumption of fathead minnows (*Pimephales promelas*) in prairie wetlands: a bioenergetics approach. Canadian Journal of Fisheries and Aquatic Sciences 54:15–27.

Dvorak, J., G. Imhof, J. W. Day, Jr., R. Hacker, J. Holicik, K. Hudec, J. Pelikan, and E. Opatrny. 1998. The role of animals and animal communities in wetlands. p. 211–318. *In* D. F. Westlate, J. Kvet, and A. Szczepanski (eds.) The Production Ecology of Wetlands. Cambridge University Press, New York, NY, USA.

Eadie, J. M., M. L. Mallory, and H. G. Lumsden. 1995. Common goldeneye (*Bucephala clangula*). The Birds of North America, Number 170. The American Ornithologists' Union, Washington, DC, USA. and the Academy of Natural Sciences, Philadelphia, PA, USA.

Euliss, N. H., Jr. and G. Grodhaus. 1987. Management of midges and other invertebrates for waterfowl wintering in California. California Fish and Game 73:238–43.

Euliss, N. H., Jr., J. W. LaBaugh, L. H. Fredrickson, D. M. Mushet, M. K. Laubhan, G. A. Swanson, T. C. Winter, D. O. Rosenberry, and R. D. Nelson. 2004. The wetland continuum: a conceptual framework for interpreting biological studies. Wetlands 24:448–58.

Galatowitsch, S. M. and A. G. van der Valk. 1994. Restoring Prairie Wetlands: An Ecological Approach. Iowa State University Press, Ames, IA, USA.

Gleason, R. A. and N. H. Euliss, Jr. 1998. Sedimentation of prairie wetlands. Great Plains Research 8:97–112.

Gleason, R. A., N. H. Euliss, Jr., D. E. Hubbard, and W. G. Duffy. 2003. Effects of sediment load on emergence of aquatic invertebrates and plants from wetland soil egg and seed banks. Wetlands 23:26–34.

Gorham, E., W. E. Dean, and J. E. Sanger. 1983. The chemical composition of lakes in the north-central United States. Limnology and Oceanography 28:287–301.

Grue, C. E., M. W. Tome, G. A. Swanson, S. M. Borthwick, and L. R. DeWeese. 1988. Agricultural chemicals and the quality of prairie-pothole wetlands for adult and juvenile waterfowl – what are the concerns? p. 55–64. *In* P. J. Stuber (ed.) Proceedings National Symposium of Protection of Wetlands from Agricultural Impacts. U.S. Department of Interior, U.S. Fish and Wildlife Service, Biological Report 88(16).

Hanson, M. A. and M. G. Butler. 1994. Response of food web manipulation in a shallow waterfowl lake. Hydrobiologia 279/280: 457–66.

Hanson, M. A. and M. R. Riggs. 1995. Potential effects of fish predation on wetland invertebrates: a comparison of wetlands with and without fathead minnows. Wetlands 15:167–75.

Hanson, M. A., K. D. Zimmer, M. G. Butler, B. A. Tangen, B. R. Herwig, and N. H. Euliss, Jr. 2005. Biotic interactions as determination of ecosystem structure in prairie wetlands: an example using fish. Wetlands 25:764–75.

Johnson, R. R. and K. F. Higgins. 1997. Wetland resources of eastern South Dakota. South Dakota State University, Brookings, South Dakota, USA.<http://www.npwrc.usgs.gov/resource/wetlands/sdwet/sdwet.htm>

Kantrud, H. A. 1992. History of cattails on the prairies: wildlife impacts. p. 9–12. In G. M. Linz (ed.) Proceedings of the Cattail Management Symposium, Fargo, ND, USA.<http://www.npwrc.usgs.gov/resource/plants/cattail/cattail.htm>.

Kantrud, H. A., G. L. Krapu, and G. A. Swanson. 1989. Prairie basin wetlands of North Dakota: a community profile. Biological report 85(7.28). U.S. Department of the Interior, Fish and Wildlife Service, Research and Development, Washington, DC, USA.

Krapu, G. L. and K. J. Reinecke. 1992. Foraging ecology and nutrition. p. 1–29. In B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L.. Krapu (eds.) Ecology and Management of Breeding Waterfowl. University of Minnesota Press, Minneapolis, MN, USA.

Krull, J. H. 1970. Aquatic plant-macroinvertebrate associations and waterfowl. Journal of Wildlife Management 34:707–18.

La Peyre, M. K., M. A. Reams, and I. A. Mendelssohn. 2001. Linking actions to outcomes in wetland management: an overview of U.S. state wetland management. Wetlands 21:66–74.

Lindeman, D. H. and R. G. Clark. 1999. Amphipods, land-use impacts, and lesser scaup (Aythya affinis) distribution in Saskatchewan wetlands. Wetlands 19:627–38.

Low, J. B. 1941. Spring flight of diving ducks through northwestern Iowa. Condor 43:142–51.

Luo, H.-R., L. M. Smith, B. L. Allen, and D. A. Haukos. 1997. Effects of sedimentation on playa wetland volume. Ecological Applications 7:247–52.

MacNeil, C., J. T. A. Dick, and R. W. Elwood. 1999. The dynamics of predation on Gammarus spp. (Crustacea: Amphipoda). Biological Reviews of the Cambridge Philosophical Society 74:375–95.

Martin, D. B. and W. A. Hartman. 1987. The effect of cultivation on sediment composition and deposition in prairie pothole wetlands. Water, Air, and Soil Pollution 34:45–53.

Murkin, H. R. 1989. The basis for food chains in prairie wetlands. p. 316–39. In A. G. van der Valk (ed.) Northern Prairie Wetlands. Iowa State University Press, Ames, IA, USA.

Murkin, H. R. and L. C. M. Ross. 2000. Invertebrates in prairie wetlands. p. 201–48. In H. R. Murkin, A. G. van der Valk, and W. R. Clark (eds.) Prairie Wetland Ecology: The Contribution of the Marsh Ecology Research Program. Iowa State University Press, Ames, IA, USA.

Neill, C. and J. C. Cornwell. 1992. Stable carbon, nitrogen, and sulfur isotopes in a prairie marsh food web. Wetlands 12:217–24.

Nyman, J. A. and R. H. Chabreck. 1996. Some effects of 30 years of weir-management on coastal marsh aquatic vegetation and implications for waterfowl management. Gulf of Mexico Science 1:16–25.

Olenick, R. J. and J. H. Gee. 1981. Tiger salamanders (Ambystoma tigrinum) and stocked rainbow trout (Salmo gairdneri): potential competitors for food in Manitoba prairie pothole lakes. Canadian Field-Naturalist 95:129–32.

Peterka, J. J. 1989. Fishes in northern prairie wetlands. p. 302–15. In A. G. van der Valk (ed.) Northern Prairie Wetlands. Iowa State University Press, Ames, IA, USA.

Pickard, D. P. and A. C. Benke. 1996. Production dynamics of Hyalella azteca (amphipoda) among different habitats in a small wetland in the southeastern USA. Journal of the North American Benthological Society 15:537–50.

Rogers, J. P. and L. J. Korschgen. 1966. Foods of lesser scaups on breeding, migration, and wintering areas. Journal of Wildlife Management 30:258–64.

Salki, A. G. 1981. The crustacean zooplankton communities of three prairie lakes subject to varying degrees of anoxia. M.S. Thesis. University of Manitoba, Winnipeg, Manitoba, Canada.

SAS Institute. 2002. SAS/STAT user's guide, version 9. SAS Institute, Cary, NC, USA.

Saxton, A. M. 1998. A macro for converting mean separation output to letter groupings in Proc Mixed. p. 1243–46. In Proceedings of the 23rd annual SAS Users Group International Conference. SAS Institute, Cary, NC, USA.

Scheffer, M., S. H. Hosper, M. L. Meijer, B. Moss, and E. Jeppesen. 1993. Alternative equilibria in shallow lakes. Trends in Ecology and evolution 8:275–79.

Schriver, P., J. Bogestrand, E. Jeppesen, and M. Sondergaard. 1995. Impact of submerged macrophytes on fish-zooplankton-phytoplankton interactions: large-scale enclosure experiments in a shallow eutrophic lake. Freshwater Biology 33:255–70.

Strand, K. A. 2005. Diet and body composition of migrating lesser scaup (Aythya affinis) in Eastern South Dakota. M.S. Thesis. South Dakota State University, Brookings, SD, USA.

Strayer, D. L. and H. M. Malcom. 2007. Submersed vegetation as habitat for invertebrates in the Hudson River Estuary. Estuaries and Coasts 30:253–64.

Swanson, G. A. and H. F. Duebbert. 1989. Wetland habitats of waterfowl in the prairie pothole region. p. 228–67. In A. G. van der Valk (ed.) Northern Prairie Wetlands. Iowa State University Press, Ames, IA, USA.

Swanson, G. A. and H. Nelson. 1970. Potential influence of fish rearing programs on waterfowl breeding habitat. p. 65–71. In E. Schneberger (ed.) Symposium on the Management of Midwestern Winterkill Lakes. North Central Division of the American Fisheries Society, Winnipeg, Manitoba, Canada.

Tanner, C. B. and M. L. Jackson. 1947. Nomographs of sedimentation times for soil particles under gravity or centrifugal acceleration. Soil Science Society Proceedings 12:60–65.

Tome, M. W., C. E. Grue, and M. G. Henry. 1995. Case studies: effects of agricultural pesticides on waterfowl and prairie pothole wetlands. p. 565–76. In D. J. Hoffman, B. A. Rattner, G. A. Burton, Jr., and J. Cairns, Jr. (eds.) Handbook of Ecotoxicology. Lewis Publishers, CRC Press, Boca Raton, FL, USA.

U.S. Environmental Protection Agency. 1995. National water quality inventory: 1994 report to Congress. EPA Report 841-R-95-005. U.S. Environmental Protection Agency, Washington, DC, USA.

U.S. Fish and Wildlife Service. 2005. Waterfowl population status, 2005. U.S. Department of the Interior, U.S. Fish and Wildlife Service, Washington, DC, USA.

Wellborn, G. A. 1994. Size-biased predation and prey life-histories – a comparative-study of fresh-water amphipod populations. Ecology 75:2104–17.

Wen, Y. H. 1992. Life history of Hyalella azteca (Crustacea: Amphipoda) in a hypereutrophic prairie pond in southern Alberta. Canadian Journal of Zoology 70:1417–24.

Wooster, D. E. 1998. Amphipod (Gammarus minus) responses to predators and predator impact on amphipod density. Oecologia 115:253–59.

Zimmer, K. D., M. A. Hanson, and M. G. Butler. 2000. Factors influencing invertebrate communities in prairie wetlands: a multivariate approach. Canadian Journal of Fisheries and Aquatic Sciences 57:76–85.

Zimmer, K. D., M. A. Hanson, and M. G. Butler. 2001. Effects of fathead minnow colonization and removal on a prairie wetland ecosystem. Ecosystems 4:346–57.

Zimmer, K. D., M. A. Hanson, and M. G. Butler. 2002. Effects of fathead minnows and restoration on prairie wetland ecosystems. Freshwater Biology 47:2071–86.