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High abundance of a single taxon (amphipods) predicts aquatic macrophyte biodiversity in prairie wetlands

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Abstract

Conservation programs often aim to protect the abundance of individual species and biodiversity simultaneously. We quantified relations between amphipod densities and aquatic macrophyte (large plants and algae) diversity to test a hypothesis that biodiversity can support high abundance of a single taxonomic group. Amphipods (*Gammarus lacustris* and *Hyalella azteca*) are key forage for waterfowl and are declining in the Prairie Pothole Region of North America. We sampled a large gradient of amphipod densities (0–7050 amphipods/m³) in 49 semi-permanent wetlands, and 50% of the study wetlands had high amphipod densities (> 500 amphipods/m³). Generalized linear models revealed *G. lacustris* and *H. azteca* densities increased exponentially with macrophyte diversity indices. Further, *H. azteca* densities were greatest at moderate levels of submersed vegetation biomass. Community analyses showed both amphipod species were positively associated with diverse macrophyte assemblages and negatively associated with high coverage of cat-tails (*Typha* spp.), a taxon that creates monotypic stands, as well as bladderwort (*Utricularia* spp.), a carnivorous plant. Our results indicate that amphipods could be used as an umbrella species for protecting diverse macrophyte communities in semi-permanent and permanent wetlands of North America's Prairie Pothole Region.

Keywords Amphipoda · Aquatic vegetation · Systematic conservation planning · Umbrella species · Waterfowl

Introduction

Systematic conservation planning has focused on maintaining, protecting, and restoring biodiversity. The systematic conservation planning model is used worldwide to identify and prioritize landscape conservation networks (Margules and Pressey 2000). Planners

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first choose which conservation proxies, such as ecosystem functions or species, will be used to represent biodiversity (Bal et al. 2018). Biodiversity proxies often include individual taxonomic groups that are easy to measure and are environmentally sensitive (“indicator” species) and taxa whose protection will extend to a wide range of co-occurring species (“umbrella” species). Decadal long debates continue as to whether a single-species focus can conserve biodiversity (Simberloff 1998; Runge et al. 2019). More scientific evidence linking single species abundance and biodiversity may provide opportunities to combine these conservation strategies (Lindenmayer et al. 2007).

The implied idea of managing the abundance of specific species for conserving biodiversity or vice versa is paradoxical. So, a key question remains: is the conservation of *biodiversity* at odds or compatible with the conservation of the *abundance of a single species*? We evaluated this question by examining the role of wetland macrophyte diversity in supporting abundant populations of amphipods, which are a key food resource for many waterfowl and other wetland wildlife (Olenick and Gee 1981; Afton and Hier 1991; Benoy et al. 2002). Similarly, we explored whether amphipods could be an *umbrella species* (i.e., whose protection would extend to a large number of other species, such as macrophyte diversity). Identifying more umbrella species can help to address global freshwater biodiversity loss (Kalinkat et al. 2017) by prioritizing conservation reserves and evaluating the effectiveness of restoration.

Amphipods (*Gammarus lacustris* and *Hyaella azteca*) are wetland crustaceans of known ecological significance to waterfowl (Afton et al. 1991) that are easy to detect when found in high densities (Fig. 1a–c). However, it remains unclear whether amphipod abundance indicates ecosystem health (such as high diversity) and whether a conservation focus on this taxonomic group might also enhance wetland biodiversity. Amphipods are an especially important forage base for some waterfowl species such as Lesser and Greater Scaup (*Aythya affinis* and *A. marila*, respectively), hereafter scaup (Afton et al. 1991). Brood-rearing and migrating scaup preferentially inhabit wetlands (Fast et al. 2004; Anteau and Afton 2009; Kahara and Chipps 2009), and scaup forage most efficiently in wetlands with high amphipod densities (Anteau and Afton 2009).

Several studies have shown amphipod abundances have declined across the Prairie Pothole Region (PPR) of North America in the past few decades (Afton and Hier 1991; Anteau and Afton 2008a, b; Strand et al. 2008), which likely cascaded to partially cause scaup population declines (Anteau and Afton, 2006, 2008b; Austin et al., 2000). Previous studies showed amphipod densities are negatively correlated with fish densities (Hanson and Butler 1994; Anteau et al. 2011) and high hydrologic connectivity that allows fish passage into wetlands (Wiltermuth 2014). Amphipod densities are also correlated with moderate concentrations of organic suspended sediments and the abundance of submersed macrophytes (Kahara and Chipps 2009; Anteau et al. 2011) but not with upland cultivation or vegetation buffer widths (Janke et al. 2019). This body of previous work was informative but limited because it included few study wetlands with high densities of amphipods (Anteau and Afton 2008a). Occasionally wetlands in the PPR still host high amphipod densities (> 500 amphipods/m³); however, little is known of the factors driving wetland habitat suitability for these high densities despite the importance of understanding those drivers to protect or enhance available habitat (Kahara and Chipps 2009; Larson et al. 2018).

Our research objective was to understand the association between macrophyte species diversity and high densities of amphipods (*G. lacustris* and *H. azteca*). We hypothesized that macrophyte diversity and amphipod abundance would be positively correlated because diversity may increase system productivity that could support amphipod forage

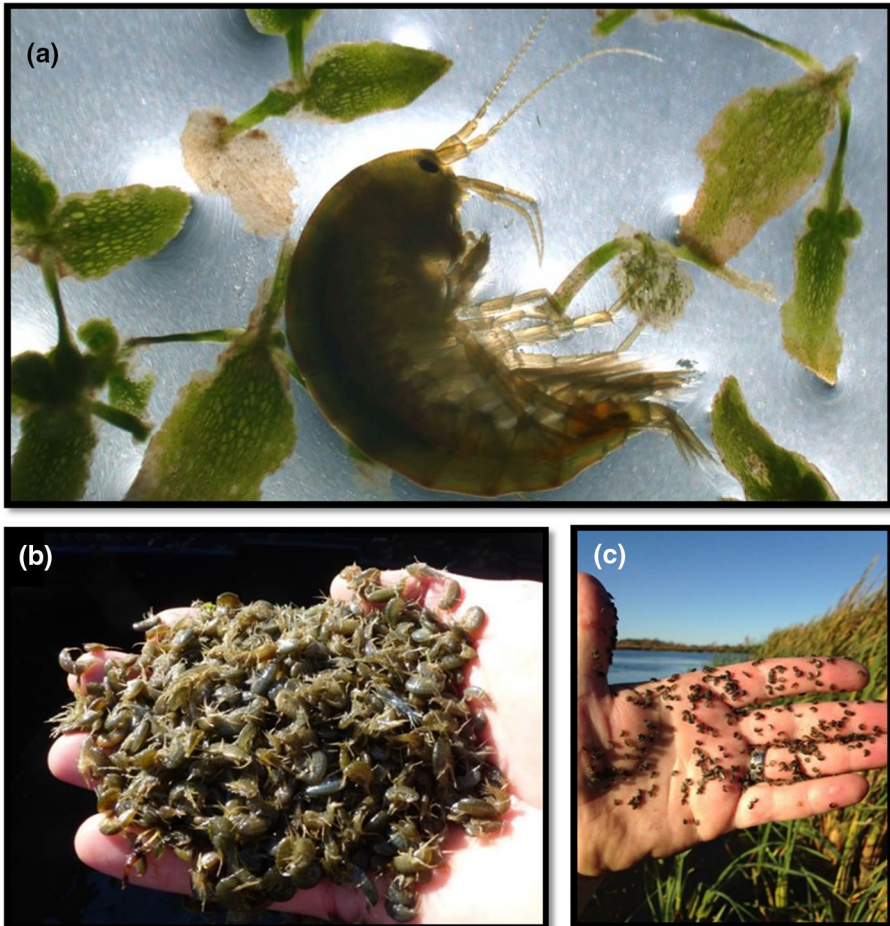


Fig. 1 Photographs of the amphipod *Gammarus lacustris* and the aquatic plant *Lemna trisulca* under 60×microscopy (panel **a**); a handful of *Gammarus lacustris* (panel **b**) and *Hyaella azteca* (panel **c**), both taken from natural wetlands with high amphipod densities (> 500 amphipods m^{-3}) in the Prairie Pothole Region, Minnesota, USA. Photographs taken by Breanna Keith (panel **a**), Danelle Larson (panel **b**), and Robert Baden (panel **c**), all used with permission

and because other factors such as water quality are interrelated. Further, we hypothesized that high amphipod abundance would be positively correlated to both submersed plant biomass and emergsed cattail fringe because these plant resources could provide refuge from predation and a carbon-rich food source. We explored the idea that amphipods could be used as umbrella species because we hypothesized amphipods would have several characteristics of an umbrella species: (1) easy to detect in high densities, (2) are environmentally sensitive to factors such as water quality and macrophytes, and (3) amphipod conservation and management could likely extend to many other species (such as macrophyte diversity).

Methods

Study sites and design

We studied 49 small wetlands within the Prairie Pothole Region and forest-transition zone of Minnesota, U.S.A. Past research used random-sample approaches, which highlighted the lack of amphipod presence in most Minnesota wetlands and occasionally wetlands with very high densities (Anteau and Afton 2008a; Anteau et al. 2011). Those prior studies connected amphipod abundance with environmental conditions but contained few study sites with very high amphipod densities, thus limiting their inferential value for the environmental conditions of wetlands containing high amphipod densities. Therefore, our study design intentionally targeted wetlands with a range of amphipod densities, especially high densities not captured with previous studies. We randomly selected half of our study wetlands, and the other half were targeted to have high densities of any amphipod species. The high-density wetlands were identified through personal communications with eight resource managers in our study region, as well as the published reports by Anteau and Afton (2008a, 2009) and Janke (2016). A subsequent rapid assessment of amphipod density in spring 2018 at 111 candidate basins confirmed that 24 wetlands had > 500 amphipods/m³, which we included in this study as high-density wetlands based on expert opinion by the authors and resource managers. The other 25 study wetlands with unknown amphipod presence and density were randomly selected with ArcGIS software the following criteria: (1) located within a 24 km radius of high-density wetland; (2) a semi-permanent or permanent water body where amphipods can persist (Anteau et al. 2011); and (3) similar ($\pm 25\%$) wetland surface area as the selected high-density wetlands. The intention of this selection criteria was to increase the likelihood of finding amphipods in suitable hydrology (semi-permanent yet shallow) and ease of sampling (e.g., not driving long distances between sites). The design was not a “paired design” because the wetlands were independent of one from another and not meaningfully matched pairs.

The 49 wetlands represented a variety of amphipod densities (0–7050 amphipods/m³), land uses (including forested, native prairie, and agricultural cultivation), land ownership (including private wetlands, state lands, federal lands, and mixtures of ownership), wetland sizes (0.4–77 ha), average water depths (72–164 cm, excluding one outlier of 604 cm), water quality conditions, and macrophyte metrics and communities (see ‘Results’ below and the complete dataset [Larson et al. 2021]).

Field data collection

Amphipods were sampled in April and May 2019. We targeted adult amphipods and this sampling time because adults are easy to capture and identify as compared to juveniles that can be small and inconspicuous and to avoid detection error from high macrophyte biomass in summer. We sampled a total of eight stratified random sampling locations at each wetland. The strata included near-shore points (within ~5 m of shore or the outermost ring of impassable emerged vegetation) and deeper points (~50 m from shore) to capture a range of habitats. Using ArcMap (release 10; ESRI, Redlands, California, USA), we generated eight equally spaced transects that ran perpendicular to the longest axis of the wetland. Each transect contained one sample point, alternating between near-shore points and deeper points. The sample points were preprogrammed into a Garmin 76 GPS unit for field navigation (~3-m positional accuracy). Sampling was limited to points with a maximum

depth of 1.4 m due to sweep net limitations. Alternate points along the transect were sampled when water depth was > 1.4 m or the near-shore point was > 5 m from shore.

Separate water column and benthic samples were collected using sweep nets (mesh size: 1200 microns). Benthic samples were obtained by sweeping a D-frame net (net diameter: 0.0647 m²) for 0.5 m along the wetland bottom to capture the top ~ 3 cm of sediment and organisms. Water column samples were collected with a D-frame or circular sweep net (net diameter: 0.0452 m²) that was bent 90° so the net opening was perpendicular to the handle. We plunged the sweep net to a depth of 30 cm (the benthic net height) above the benthos in an area undisturbed by the benthic sweep, moved the net horizontally to undisturbed water, and raised the net vertically out of water. During the plunge the net was inverted, so a sample was only collected during the vertical retrieve. Samples were drained of excess water and preserved in 95% ethanol. Samples were transported to the Minnesota Department of Natural Resources' Wetland laboratory and processed within four months of collection.

We conducted comprehensive wetland habitat surveys once in July 2019 to capture representative wetland conditions and peak macrophyte species richness. Water samples were collected near the center of each wetland in 50-mL polypropylene sterile tubes, stored on ice in a cooler, and shipped on ice to the Minnesota Department of Agriculture Laboratory Services for analyses of total phosphorus (P). Wetland pH (Hach® HQ40d, Loveland, Colorado, USA) and turbidity (Hach® 2100P, Loveland, Colorado, USA) were also measured near the center of each wetland.

We sampled water depth and aquatic macrophytes (submersed aquatic vegetation [SAV], emersed, rooted-floating, and free-floating life forms) at evenly spaced, random sampling points. These sample points differed from where amphipods were collected, and so the depth and macrophyte data represent the entire wetland and not a sampling point. The entire wetland was gridded in ArcMap, and each grid provided a sampling point for water depth and vegetation. Grid size varied by wetland size; wetlands < 4 ha had 10 sampling points, and we increased sampling by one point for each additional 0.5 ha. The number of sampling points per wetland ranged from 10 to 67 (average: 25 points). We navigated via canoe to each sampling point using a Garmin 76 GPS unit. At each point, we measured water depth and dragged one plant rake of 35-cm circular diameter along the bottom of the wetland for 150 cm. We used a relative biomass index to estimate the total amount of submersed plants and filamentous algae on the rake (ordinal score ranging from 0 to 4; Online Appendix 1) and then identified each species present using identification keys (Skawinski 2018). We quantified emersed vegetation prevalence along shorelines using visual field surveys in which we recorded the presence of emersed vegetation guilds (including cattail, bulrush, and sedge/rush) at the end of each vegetation sampling transect line. Data from the individual points were compiled for each wetland to calculate average biomass and species-specific prevalence. We acknowledge that high wetland plant diversity occurs in the emergent and wet meadows on the upland periphery from the permanent water, but our assessments did not include species-level identification of shallow marsh plants principally because these are not the common habitats that amphipods reside in. Although fish abundance is known to be negatively correlated to amphipods, this study focused on the relations between macrophytes, water quality, and amphipods and not fish. Fish were not sampled as part of this study but may have been present.

Laboratory analyses

Sample contents were washed in a 500- μm rectangular sieve to remove fine sediments. All material on the sieve was suspended gently in a bucket of water to evenly disperse the contents. A grid was placed over the sieve to allow for sub-sampling. We picked a minimum of 25% of the sample on the sieve and added more grids until at least 400 invertebrates were picked or the entire sample was processed. All picked invertebrates were stored in 70% ethanol for identification and archiving.

We enumerated and identified all amphipods to the species-level using taxonomic keys (Merritt et al. 2008; Glazier 2014) by using a lighted trinocular microscope with 110 \times magnification potential. Amphipod counts were scaled to the entire sample if they had been subsampled. Amphipod abundance was the total number of individuals counted at each wetland ($n=8$ standardized sweeps). Average amphipod density (units: $\#/m^3$) was calculated for each basin by dividing the basin-level abundance by the volume of water passed through the sweep net.

Data analyses

We averaged amphipod counts and density by wetland as response variables because the wetland was the experimental unit where samples were truly independent. Therefore, the inferences of amphipods and habitat associations were at the wetland-scale and not at the point of amphipod sampling. We calculated a variety of α -biodiversity facets, including Simpson diversity index, Shannon diversity index, Pielou's evenness index, and species richness using all vegetation species or guilds collected.

Three species of amphipods were collected in our study wetlands: *G. lacustris*, *H. azteca*, and *Crangonyx* spp. We chose to model *G. lacustris* and *H. azteca* separately because each species may respond differently to environmental predictors. We did not analyze *Crangonyx* spp. due to infrequent occurrences (<15%) and low densities (Table 1, Fig. 2).

We used two complementary analyses to infer biologically and statistically significant factors that influenced amphipod abundance: (1) generalized linear models to test our hypotheses that amphipod density would relate positively to SAV biomass, macrophyte diversity, and emerged vegetation prevalence along shorelines, and (2) a redundancy analysis (RDA) of amphipod abundance and macrophyte assemblages to test species affiliations. We reported the p -value with degrees of freedom and relative magnitude of differences to assess 'statistical significance' of model outputs. The statistical analysis outputs, graphical trends, and previous literature were used to conclude what constitutes 'biologically significant' results and where uncertainty remains (Wasserstein et al. 2019).

All models and graphs were produced using software R 4.0.5 (R Foundation for Statistical Computing 2018). We modeled species-specific amphipod counts to our predictor variables using a negative binomial distribution with a log link function using the 'MASS' package (Ripley et al. 2020); prior models with Poisson distribution of transformed data were over dispersed and thus not reported. We used the natural log of water-volume swept (m^3 ; summed per wetland) as an offset variable. The predictor variables included the three primary hypotheses about the influence of macrophytes on amphipods: (1) macrophyte diversity (all life forms); (2) SAV biomass; and (3) the percentage of shoreline rimmed by emerged vegetation. We also included several covariates to account for wetland-to-wetland

Table 1 The summary statistics of densities of each amphipod genus detected in the study ($n=49$ wetlands), which includes randomly selected wetlands, intentionally selected wetlands with known high densities (>500 amphipods m^{-3}) of at least one species of amphipod, and the combined summaries of both wetland selection types

Genus	Minimum	1st quartile	Median	Arithmetic mean	3rd quartile	Maximum
Randomly selected wetlands ($n=25$)						
Cragonyx	0	0	0	1	0	23
Gammarus	0	0	0	12	0	200
Hyalabella	0	0	19	189	102	1329
Intentionally selected, 'high density' wetlands ($n=24$)						
Cragonyx	0	0	0	16	15	124
Gammarus	0	58	422	681	1050	2736
Hyalabella	0	70	321	1001	1259	7050
All study wetlands ($n=49$)						
Cragonyx	0	0	0	9	3	124
Gammarus	0	0	15	353	422	2736
Hyalabella	0	13	77	620	734	7050

variability due to factors other than macrophytes. Our approach was to have a model for each amphipod species that contained at least three variables that represented each of the macrophyte hypotheses and then interpreted the strength of their support by examining the parameter estimates, 95% confidence limits, and p -values.

We took several steps to select the variables used in the final models. These steps included examining plots of the raw data, transforming data as necessary, and then performing a single-variable elimination. We assessed relative goodness of fit and parsimony by comparing the Type III likelihood ratio statistic, and single variables were eliminated if its p -value was >0.05 . We plotted species' density against each potential variable to identify non-linear relations and any needs for transformations. The *H. azteca* densities graphically appeared to increase with SAV biomass up to a point then decreased, so we included a quadratic effect. The covariates we initially considered were maximum depth, wetland area, pH, total P, turbidity, and an index of suspended sediments. There were low correlations ($r < 0.4$) among these covariates and our three hypothesized variables, with exception of turbidity and total P ($r = 0.49$). We suspected that our turbidity measurement was composed of phytoplankton and suspended sediments, which could be an important covariate based on Anteau et al. (2011). So, like Anteau et al. (2011), we ran a regression using total P to predict turbidity ($\text{Turbidity} = 0.94 + 75.48 \times \text{total P}$; $r^2 = 0.23$) and used the residuals of that regression to index suspended sediments. The resulting suspended-sediment index was orthogonal with total P. For *G. lacustris*, the plots indicated total P should be transformed with a natural log, and there were threshold effects of maximum depth (~ 150 cm) and wetland area (15 ha); so, we indexed maximum depths > 150 cm as "1" and ≤ 150 as "0" and wetland areas > 15 ha as "1" and ≤ 15 as "0." For *H. azteca*, we did not consider maximum depth, wetland area, total P, and suspended-sediment index because preliminary analyses indicated no pattern with their densities. Lastly, we chose a single, most informative variable to represent the three hypotheses related to macrophyte diversity, biomass,

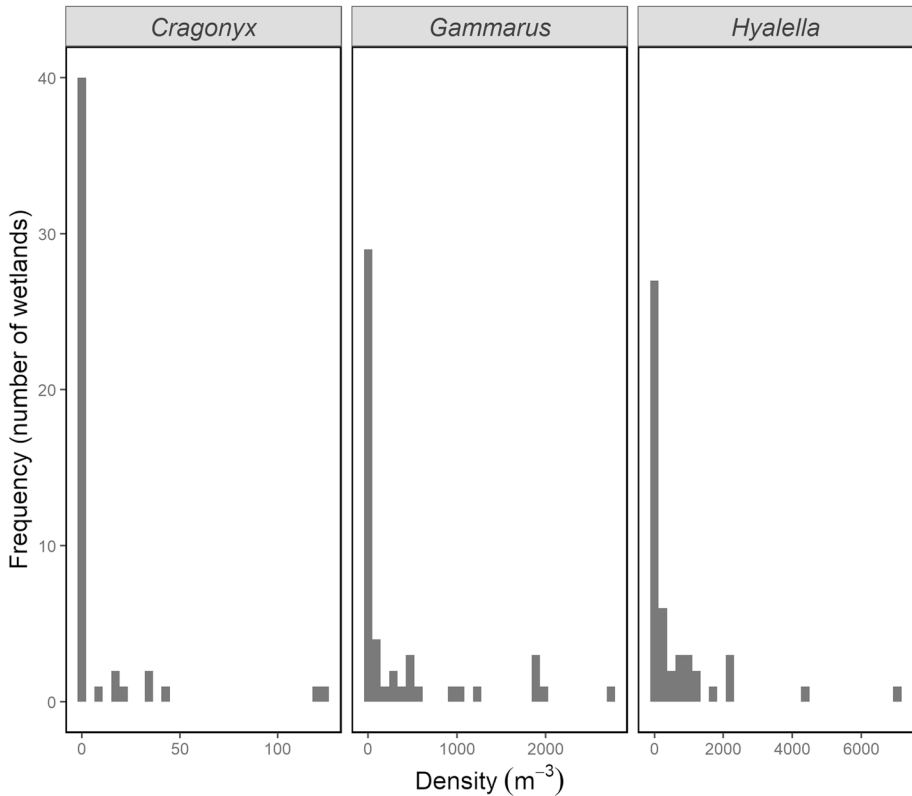


Fig. 2 Histograms showing the frequency of amphipod densities measured in 49 wetlands in the Prairie Pothole Region, Minnesota USA in spring 2019

and emergent vegetation in the models. For both amphipod species, the SAV biomass index was more informative than SAV prevalence. Simpson's diversity index was more informative than Shannon's diversity index, species richness, or Pielou's evenness. Shoreline emerged prevalence was a better predictor than total wetland emerged prevalence.

We reported results of full models that included the three hypothesized macrophyte variables and informative covariates (see Tables 2 and 3). To assess model fits, we used marginal model plots (Online Appendix 2) that compare the data and model fits. We calculated the predicted values of amphipod density of our hypothesized variables while holding the other covariates constant and provided graphs of each model's predictions (Figs. 3 and 4).

In addition, we conducted a redundancy analysis to examine relations among species-specific amphipod counts and macrophyte assemblages using the 'vegan' package in software R (Oksanen et al. 2019). This analysis is a multivariate extension of multiple regression where the ecological community is constrained by linear combinations of the predictor variables. The two amphipod species were used as separate response variables. Predictor variables included prevalence for the eight most common SAV species, one prevalent emerged species (*Typha* spp.), and filamentous algae (not speciated). The aquatic vegetation species matrix did not have ecological transformations, but we ln-transformed the amphipod count data to fit linear assumptions. We conducted a permuted, multivariate

Table 2 Analysis results of maximum likelihood parameter estimates for *Gammarus lacustris*

Parameter	DF _{num} , DF _{den}	Estimate	Standard error	Wald 95% confidence limits		Wald χ^2	p-value
Intercept	1, 40	1.54	2.97	-4.28	7.36	0.27	0.604
Simpson diversity	1, 40	13.16	3.31	6.68	19.63	15.85	<0.001
SAV biomass	1, 40	-1.45	0.45	-2.34	-0.56	10.13	0.002
Shoreline emergent prevalence	1, 40	-0.02	0.02	-0.06	0.02	1.25	0.265
Maximum water depth	1, 40	1.77	0.88	0.04	3.49	4.02	0.045
Wetland size	1, 40	-4.33	1.11	-6.51	-2.15	15.15	<0.001
Total P	1, 40	1.05	0.53	0.00	2.09	3.87	0.049
Suspended sediment	1, 40	0.14	0.06	0.02	0.26	4.89	0.027
Dispersion	1, 40	3.71	0.95	2.25	6.11	NA	NA

The parameters included in this table were of primary interest with hypotheses of positive associations of *G. lacustris* and aquatic vegetation. Parameters in bold were primary hypothesized variables of interest related to aquatic vegetation and the others were covariates of secondary interest and included to improve parameter estimates

Table 3 Analysis results of maximum likelihood parameter estimates for *Hyalella azteca*

Parameter	DF _{num} , DF _{den}	Estimate	Standard error	Wald 95% confidence limits		Wald χ^2	p-value
Intercept	1, 42	-18.87	4.90	-28.48	-9.25	14.79	<0.001
Simpson diversity	1, 42	3.20	1.32	0.59	5.79	5.80	0.016
SAV biomass	1, 42	2.90	0.96	1.00	4.79	8.97	0.003
SAV biomass × SAV biomass	1, 42	-0.80	0.23	-1.24	-0.36	12.74	<0.001
Shoreline emergent prevalence	1, 42	0.01	0.01	-0.01	0.03	0.54	0.464
pH	1, 42	2.23	0.54	1.18	3.28	17.30	<0.001
Dispersion	1, 42	2.28	0.55	1.93	4.15	NA	NA

The parameters included in this table were of primary interest with hypotheses. Parameters in bold were primary hypothesized variables of interest related to aquatic vegetation and the others were covariates of secondary interest and included to improve parameter estimates

analysis of variance ($perm = 9999$) to assess the statistical significance of the overall RDA model, axes, and terms.

Results

Amphipod densities and species co-occurrences

Our surveyed wetlands comprised a large range of amphipod densities (0–7050 amphipods/m³). Several wetlands included exceptionally high density (Table 1, Figs. 1 and 2); half of the wetlands had >500 amphipods/m³ (per the study design). Of the 25 randomly selected

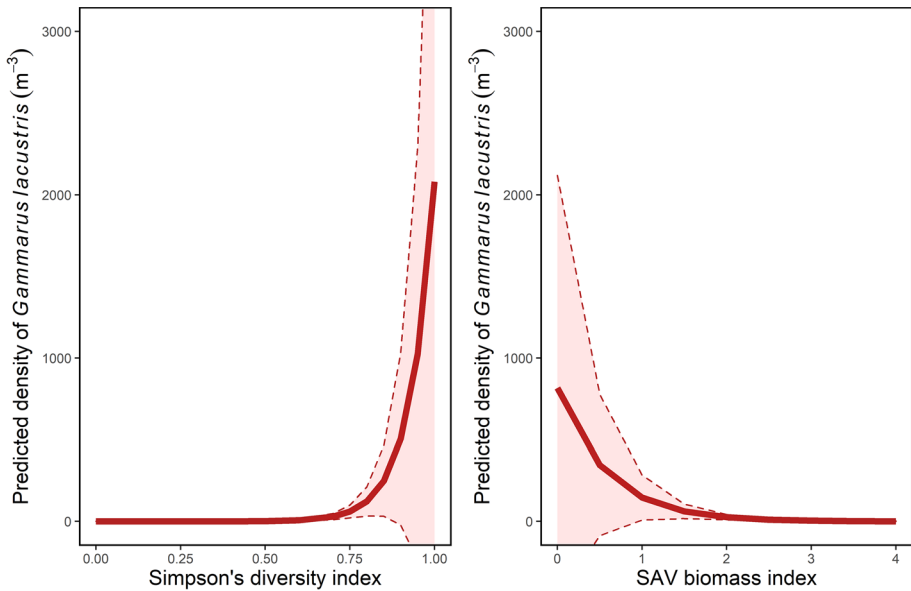


Fig. 3 The model-predicted densities of *Gammarus lacustris* in response to wetland vegetation diversity (Simpson diversity index) and submersed aquatic vegetation biomass (SAV biomass index). Shaded areas correspond to the prediction's 95% confidence intervals while other model covariates were held constant at their means

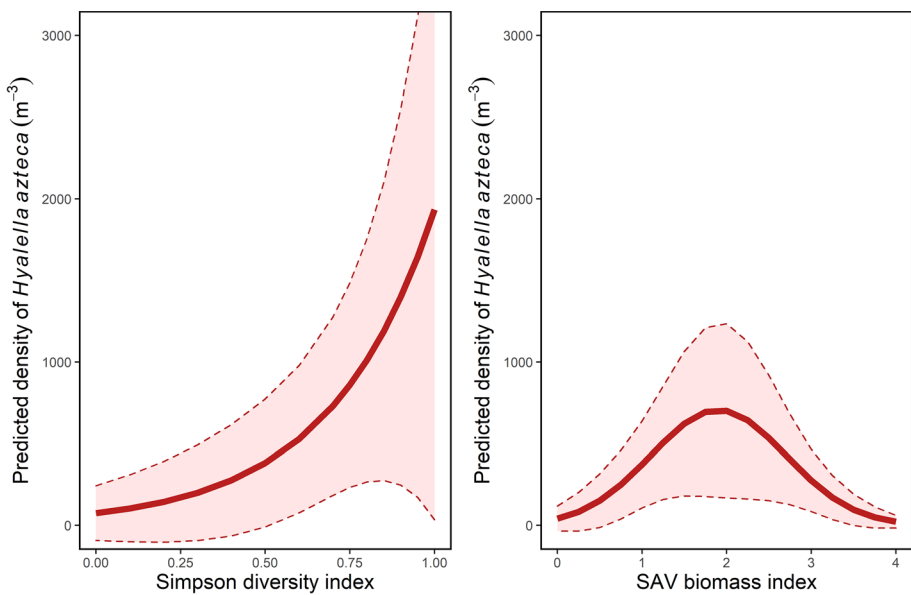


Fig. 4 The model-predicted densities of *Hyallella azteca* in response to wetland vegetation diversity (Simpson diversity index) and submersed aquatic vegetation biomass (SAV biomass index). Shaded areas correspond to the prediction's 95% confidence intervals while other model covariates were held constant at their means

wetlands, 8% had *G. lacustris* present but with relatively low densities (geometric mean: 37 *G. lacustris*/m³). The *H. azteca* were present in 70% of the 25 randomly selected wetlands (geometric mean: 63 *H. azteca*/m³), and 12% of those wetlands had relatively high density (i.e., > 500 *H. azteca*/m³).

The three amphipod species (*G. lacustris*, *H. azteca*, and *Crangonyx* spp.) typically co-occurred in wetlands, but only one species was dominant. *Gammarus lacustris* densities were not correlated with either *Crangonyx* or *H. azteca* densities ($r = -0.06$, $r = -0.02$, respectively). *Crangonyx* and *H. azteca* densities were positively correlated ($r = 0.43$).

Relationships among *Gammarus lacustris*, macrophytes, and wetland characteristics

The *G. lacustris* model was predicted by the independent variables of Simpson diversity, SAV biomass, shoreline emergent prevalence, maximum water depth, wetland size, total P, and suspended sediment (Table 2). The *G. lacustris* model predictions fit the observed data well ($r = 0.54$, Online Appendix 2A). The most informative macrophyte diversity metric (Simpson's *D*) had a strong, positive correlation with *G. lacustris* densities (Table 2, Fig. 3, Online Appendix 3B). The high-density *G. lacustris* wetlands always had a Simpson's *D* > 0.80. Although we hypothesized SAV biomass and shoreline emerged vegetation would be positively correlated with *G. lacustris* densities, the model indicated a negatively weak correlation and no correlation, respectively. The covariates showed that *G. lacustris* responded positively to wetland maximum water depth and productivity metrics but negatively to wetland size (Table 2).

Relationships among *Hyalella azteca*, macrophytes, and wetland characteristics

The *H. azteca* model was predicted by the independent variables of Simpson diversity, SAV biomass, a quadratic term for SAV biomass, shoreline emergent prevalence, and pH (Table 3). The *H. azteca* regression model fit the observed data less well than the *G. lacustris* model, but the predicted values were correlated with the observed data ($r = 0.37$). *H. azteca* were positively correlated to Simpson's diversity (Table 3, Fig. 4, Online Appendix 3D), but not as strongly as *G. lacustris* based on the parameter estimates. The high-density *H. azteca* wetlands had diversity-index values from $D = 0.5$ to 1.0. The *H. azteca* densities displayed a significant quadratic relationship with SAV biomass whereby densities were maximized at moderate SAV biomass values. Shoreline emerged prevalence was not a significant predictor variable. Only one informative covariate (pH) was included in the model, which was positively correlated with *H. azteca* densities (Table 3).

Community analysis of amphipods and macrophytes

We used redundancy analysis to examine the community composition of macrophytes to explore which species were most closely associated with amphipod abundance. The full community model was significant ($F_{1,38} = 1.82$, $p = 0.040$) as was the first axis ($F_{1,46} = 15.80$, $p = 0.043$). *Lemna trisulca* (LETR) along the first axis was a predictor of *G. lacustris* abundance ($F_{1,38} = 5.09$, $R^2 = 0.19$, $p = 0.001$) and *Myriophyllum sibiricum* (MYSI) was a predictor of *H. azteca* abundance ($F_{1,38} = 5.55$, $R^2 = 0.21$, $p = 0.005$).

Graphically, the redundancy analysis showed biologically significant relationships between macrophyte assemblages and amphipod abundance (Fig. 5). Most wetlands were

spread across ordination space (i.e., not clumped together on the graph), indicating that they had differing plant-community composition and amphipod abundances. The two amphipod species were not correlated and fell along two different ordination axes, indicating that the species often did not co-occur in the same wetlands and that each amphipod species were associated with different macrophyte assemblages. The *G. lacustris* was strongly associated with *L. trisulca* (LETR), which was positively correlated with SAV diversity and species richness but not evenness (Online Appendix 3B). The *H. azteca* was associated with macrophyte assemblages composed of predominately *Stuckenia pectinata* (STPE15), filamentous algae, *Potamogeton friesii* (POFR3), *Potamogeton zosteriformis* (POZO), and *M. sibiricum* (MYSI); these macrophyte species were also prevalent and had moderately high SAV biomass. Both amphipod species were negatively associated with high prevalence of *Typha* spp. (TYPHA) and the carnivorous plant, *Utricularia macrorhiza* (UTMA). *Chara* spp. (CHAR) and sometimes *Ceratophyllum demersum* (CEDE4) were

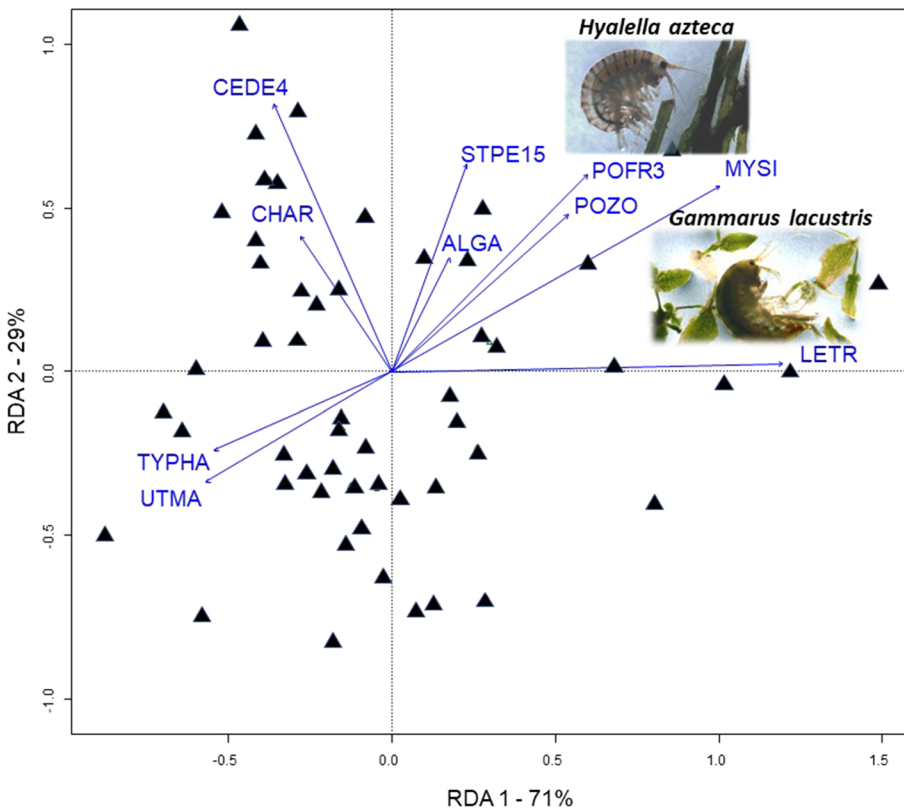


Fig. 5 A triplot of the amphipod communities and aquatic vegetation communities at 49 wetlands (triangles) in the Prairie Pothole Region, Minnesota, USA. The amphipod community in this analysis included two species: *Hyalella azteca* and *Gammarus lacustris*. The species included in the ordination included the ten most prevalent macrophytes: *Typha* spp. (TYPHA), *Utricularia macrorhiza* (UTMA), *Lemna trisulca* (LETR), *Potamogeton zosteriformis* (POZO), *Myriophyllum sibiricum* (MYSI), *Potamogeton friesii* (POFR3), *Stuckenia pectinata* (STPE15), filamentous algae (ALGA; not speciated), *Ceratophyllum demersum* (CEDE4), and *Chara* spp. (CHAR). The ordination scaling and interpretations are based on correlations; therefore, the vectors at $<90^\circ$ angles are positively correlated, vectors at 90° angles are uncorrelated/orthogonal, and vectors at 180° are negatively correlated

dominant plants (SAV species richness = 1; biomass scores = 3–4), and neither amphipod species thrived in those conditions. The results of the redundancy analysis complemented the univariate regression models (Tables 2 and 3) without conflicting results, except the redundancy analysis indicated a negative association of *Typha* spp. (TYPHA) and amphipod densities (Fig. 5).

Discussion

We found that high densities of *G. lacustris* and *H. azteca* were positively associated with macrophyte taxonomic diversity, and *G. lacustris* were especially sensitive to macrophyte diversity and other wetland characteristics. The greatest amphipod densities were found in macrophyte assemblages composed of both cosmopolitan macrophytes (e.g., *S. pectinata* and filamentous algae) and less common macrophytes (e.g., *L. trisulca*). Both amphipod species had lower densities in wetlands with high cattail (*Typha* spp.) prevalence. Our results clearly showed strong, positive correlations among amphipods and several macrophyte metrics, but the causative relationships could only be speculated. The results indicated that amphipods could be an indicator and umbrella species for wetland plant diversity; macrophyte diversity provides habitat conditions that favor high amphipod densities; macrophytes and amphipods simply require similar wetland conditions (e.g., moderate water depths and semi-permanent hydrology); and that loss of macrophyte diversity could cascade to affect amphipod abundance due to habitat loss. Regardless of which causal mechanism(s) relate amphipods and macrophyte diversity, conservation actions that support either amphipod abundance or macrophyte diversity will likely aid the other taxa (with possible caveats described further herein). Specifically, amphipods as an umbrella species may also help conserve wetland biodiversity in semi-permanent and permanent wetlands. Likewise, a conservation strategy with a focus on aquatic macrophyte communities might concomitantly result in greater amphipod abundance.

Amphipod species abundances and wetland relations differed

Hyaella azteca was much more common and abundant than *G. lacustris*, which was also the case in other Prairie Pothole Region wetlands in recent past (Anteau and Afton 2008a). Densities of *H. azteca* were often three times greater than that of *G. lacustris*, which may be partially explained by the smaller body size of *H. azteca* that allows more occupation in the same space (Thomaz and Cunha 2010). *Hyaella* also have advantageous life-history traits such as greater reproductive capacity than *Gammarus* (Glazier 2014). Although *H. azteca* were more abundant, *G. lacustris* are also ecologically significant given their high density and large body size and biomass that is important for foraging water birds (Anteau and Afton 2006).

Hyaella azteca were tolerant to a wide range of wetland conditions, whereas *G. lacustris* had a narrower and more defined ecological niche (as indicated by the number of informative covariates in the models and model fits). This result corroborates findings of Anteau and Afton (2008a, b) that *H. azteca* were generally more widespread on the landscape. In our study, *G. lacustris* were more common in small wetlands (<20 ha), were not found in average water depths <100 cm and were positively related to wetland productivity measures like total P and turbidity. Previous work demonstrated fish are more common in large, permanent Prairie Pothole Region wetlands and that fish can negatively affect

amphipod abundance (Hanson and Butler 1994; Wiltermuth 2014; Janke 2016). Therefore, our significant results on wetland size and depth may either indicate increased carrying capacity for amphipods, or reflect the unmeasured, interactive effects of fish abundance more so than wetland size or depth independently. Note our study wetlands had typically 4× lower productivity (total P and turbidity) compared to other Prairie Pothole Region wetlands in Minnesota that were classified as a degraded “turbid state” (Larson et al. 2020b), so we do not know if *G. lacustris* declines after certain productivity thresholds of eutrophication. Our findings refined niches of *H. azteca* and *G. lacustris* in relation to macrophyte communities and showed *G. lacustris* had a narrow niche breadth and is likely an environmentally sensitive species to wetland factors such as macrophyte diversity and biomass, as well as wetland size, water depth, total P, and suspended sediments.

Macrophyte biodiversity shapes the wetland that supports amphipods

Our results showed that both amphipod species were affiliated with macrophyte diversity. We suspect macrophyte diversity is indicative of overall wetland condition and supports the “biodiversity ecosystem functioning” concept (Engelhardt and Ritchie 2002; Brisson et al. 2020). Ecosystem functions provided by macrophytes to amphipods may include nutrient turnover, carbon availability, structural habitat, and water purification (Carpenter and Lodge 1986). A previous study indicated positive associations of amphipod density and stands of *Potamogeton* spp. and *L. trisulca*, but not *Chara* spp. (Hanson 1990). Our results from 49 wetlands concurred (Fig. 5) with findings from Hanson 1990 and may hint at niche-differentiation or other mechanisms linking biodiversity and amphipods.

SAV biomass

Hyalella azteca densities were maximized at moderately high macrophyte biomass whereas *G. lacustris* densities were negatively associated with SAV biomass. Total macrophyte leaf surface area and complexity from leaf branching presumably support amphipods by providing places of attachment for shelter and feeding (Thomaz and Cunha 2010). More space provided by macrophyte abundance and leaf branching is a plausible reason that the smaller-bodied *H. azteca* were often found at higher densities than the larger-bodied *G. lacustris*. Although fish can also be attracted to macrophyte beds, and the SAV biomass and complexity can reduce fish foraging effectiveness (Thomaz and Cunha 2010) and could reduce predation. We suspect *G. lacustris* were negatively associated with SAV biomass because *G. lacustris* were more common in deep wetlands, which can have less SAV due to light limitations.

Monocultures

Chara spp. and *C. demersum* were species that often dominated in high biomass, and amphipods were not typically detected in those conditions (Fig. 5). These plant species were typically found in wetlands with species richness < 2 and high SAV biomass scores from 3 to 4. We speculate the negative associations among amphipods, *Chara* spp., and *C. demersum* are related to the strong affinity of amphipods to macrophyte diversity (Figs. 3 and 4) more than the plant biomass itself. First, amphipods consume a broad array of

aquatic plants, whereas most other herbivorous aquatic invertebrates consume only one or two plant species (Newman 1991). In near monocultures, the plants senesce at the same time of year, which could reduce the availability of detritus over a long overwintering season. In contrast, a staggered timing in macrophyte senescence and varying plant decay rates could provide an ongoing refuge and detrital food base for amphipods. Further, *Chara* spp. are often encrusted with ‘marl,’ which are carbonate compounds from hard water that are slow to decompose and release carbon for detritivores. Non-native species like *Potamogeton crispus* or *Myriophyllum spicatum* can reduce macrophyte diversity and can have exceptionally high biomass, so we speculate these common invasive plants could negatively affect amphipods.

Typha × *glauca*

The emerged vegetation in this study was predominately cattails (presumably the invasive hybrid *Typha* × *glauca*), which are ecologically important but can also encroach shallow wetlands which have strong, negative ecological effects (Bansal et al. 2019). We found a weak, negative association among *Typha*, macrophyte diversity, and amphipods (Fig. 5), but our sweep-net sampling technique via canoe was insufficient for capturing amphipods in the interior of dense *Typha* beds where amphipods may reside in high density (Christensen and Crumpton 2010). Wetlands with low to moderate *Typha* prevalence are usually larger basins with enough water depth to support *G. lacustris* and dynamic water levels that prevent *Typha* dominance. *Typha* dominance is often a symptom of multiple issues, including consolidation drainage and nutrient loading (Wiltermuth and Anteau 2016; Bansal et al. 2019). The ‘hemi-marsh’ of interspersed *Typha* and open water are also beneficial to an array of water birds that feed on *G. lacustris* (Murkin et al. 1997). Management of *Typha* dominance remains a high conservation priority and challenge in North America (Bansal et al. 2019; Larson et al. 2020a, b), but may benefit *H. azteca* that resides in shallow waters where *Typha* can dominate.

Conservation strategy: using amphipods as indicators and umbrella species to protect diversity

Gammarus lacustris and possibly *H. azteca* could be indicators and umbrella species in semi-permanent and permanent wetlands in the Prairie Pothole Region because (1) both species are easy to detect and enumerate (Fig. 1a–c), (2) *G. lacustris* are particularly sensitive to environmental conditions (Table 2; Anteau and Afton 2011), and (3) their conservation might extend to a suite of other species, like macrophyte biodiversity (Tables 2 and 3). However, amphipods would not be a suitable umbrella species for naturally ephemeral wetlands that frequently dry. An important trait in an umbrella species is that species conservation can improve management decisions. A separate structured decision making approach would be warranted to fully determine the ability for management to influence amphipod populations and protect macrophyte diversity (Bal et al. 2018). Here, we provide two examples of how amphipods could be used for systematic conservation planning and watershed restoration.

Amphipod distribution mapping could be a tool for conservation planning. The ease of detecting high densities of amphipods during early spring after ice-out (Fig. 1a–c) could allow for a feasible, landscape sampling campaign. Sampling amphipods is currently a

more efficient approach to indexing wetland quality than sampling macrophyte diversity or relative fish abundance. Amphipods are easy to identify and rapidly quantify in the field, thereby negating the need for costly sample preservation and laboratory quantification. In contrast, macrophyte surveys took our team about 2–5× longer in the field and required knowledge to identify many species. However, advances in remote sensing of submersed macrophyte diversity could reduce field sampling costs and increase access to larger landscapes in the future. Previous work showed that macroinvertebrates are indicator species because they are easy to measure compared to fish and can indicate fish absence (Schilling et al. 2009). A limitation of this study is we did not sample the wet meadow vegetation diversity, which can host many species; therefore, amphipods may or may not capture diversity alterations to the shallow marsh and wet meadow plant communities. Regardless, mapping the distribution of amphipods across the Prairie Pothole Region could help managers prioritize and conserve the remaining diverse, semi-permanent wetlands in this highly degraded landscape.

Amphipods could be an indicative metric for assessing conditions of the catchment and its terminal basins, which tend to have semi-permanent and permanent hydroperiods that amphipods favor (Anteau and Afton 2011, this study). Sustained amphipod populations are limited to basins with semi-permanent and permanent hydroperiods for overwinter survival, and such basins are typically found at the catchment terminal. Managing directly for amphipod success may be difficult, but restoration of suitable wetland types specific for amphipods could extend to improving catchment health. Hydrology of these basin types is strongly affected by land use and wetland drainage throughout the catchment (McCauley et al. 2015), and in turn, the hydrology affects connectivity and macroinvertebrate communities within these terminal basins (Wiltermuth 2014). Restoration of all wetland types and wetland complexes throughout a catchment can restore natural hydroperiods of the terminal basin (Anteau 2012), and thus support amphipods. Consolidation drainage also provides more permanent water that might be favorable to amphipods, but consolidated basins are also likely to support high abundances of fish and cattails that negatively affect amphipods (Wiltermuth 2014; Wiltermuth and Anteau 2016).

Conservation strategy: managing aquatic plant diversity to provide habitat for high amphipod abundance

Our results indicated that restoring and managing wetlands for macrophyte diversity can produce habitat suitable for amphipods to thrive in high densities. Wetland restorations are often successful at simultaneously restoring hydrology, vegetation cover, and biodiversity (Galatowitsch and van der Valk 1996a; Larson et al. 2020b). Prairie wetland restorations are particularly successful at restoring the diversity of the submergent and emergent plant communities (Galatowitsch and van der Valk 1996b), and our results showed amphipod densities were strongly correlated with diversity in these plant community types. In degraded or recently restored Prairie Pothole Region wetlands, management of related wetland factors such as nutrient loading, water depth, and fish abundance is sometimes feasible and often successful for promoting macrophyte abundance and diversity (Larson et al. 2020a). Wetlands with varying water levels over space and time promote water depth requirements for amphipods and predictable, diverse macrophyte communities (Larson et al. 2020b). Major changes to the Prairie Pothole Region landscape over the past century have stabilized the water levels of many wetlands and adversely affected water clarity, macrophytes, and macroinvertebrates (McCauley et al. 2015; Wiltermuth and Anteau 2016;

McLean et al. 2019). Water level management (through intentional drawdowns) represents a strategy to mimic ecosystem processes that would otherwise remove nuisance fish, increase water quality, increase macrophyte diversity and abundance, and attract waterfowl (Hanson and Butler 1994; Larson et al. 2020a).

Our results indicated low water depths of < 100 cm during a drawdown may preclude high densities of *G. lacustris*, although the survival, growth, reproduction, and recruitment of amphipods following drawdown would warrant more study. Given the sheer number and small size of these wetlands, a possible approach for promoting variable water levels and deeper refuges for amphipod overwintering may be restoration of wetland complexes that include several hydrologic regimes. The careful application of an ecosystem-functioning based approach may preserve or restore dynamic wetland hydrology (Euliss et al. 2008), remove nuisance fish, increase macrophyte diversity, and benefit amphipods in this heavily modified landscape.

A habitat conservation strategy assumes the amphipods are not dispersal limited; if the correct habitat conditions are available (such as semi-permanent water and diverse macrophyte communities), then amphipods would relocate and establish successfully. Amphipods are likely dispersal limited because they do not have a life stage capable of flight, unlike most wetland invertebrates. Instead, amphipod dispersal is limited to transport by other organisms or flowing water and therefore dispersal depends on wetland complexes that have adequate proximity and some hydrologic connectivity. Careful evaluation of purposeful reintroduction by translocating amphipods to restored wetlands may be considered (Larson et al. 2018), and our results suggest suitable wetland habitat conditions for amphipod translocation and stocking.

Conclusions

A probable cause of amphipod and scaup abundance declines may be attributed to a loss of wetland quantity and quality (Austin et al. 2000; Anteau and Afton 2006). Using amphipods as an umbrella species may be useful for managers in identifying and prioritizing conservation for biodiversity across the Prairie Pothole Region. Likewise, the preservation and restoration of amphipod abundance may be achieved through explicit conservation and management of macrophyte diversity. The seemingly disparate strategies of conserving a single taxon (e.g., amphipods) and biodiversity (e.g., macrophyte communities) can be compatible and complementary.

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Data availability Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The peer-reviewed, analysis-ready dataset is available for public download using this citation: Larson, D.M., DeJong, D., Anteau, M.J., Fitzpatrick, M., Keith, B., Schilling, E.G., and Thoele, B., 2021, Macrophyte and amphipod surveys in prairie wetlands of Minnesota in year 2019: U.S. Geological Survey data release, <https://doi.org/10.5066/P9INBET3>.

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Declarations

Conflict of interest The author declare that they have no conflict of interest.

Ethical approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

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