

NORTH DAKOTA GAME AND FISH DEPARTMENT

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Interaction of Land Use and Wet/Dry Cycles on Invertebrate Populations in Prairie Wetlands:  
Implications for Waterbird Habitat Conservation

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**Interaction of Land Use and Climate Variability on Invertebrate Populations in Prairie Wetlands:  
Implications for Waterbird Habitat Conservation**

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**Summary**

In springs of 2010 and 2011 we sampled water depth, amphipod densities, fish abundance, and evaluated emergent vegetation structure within 153 wetlands of the Prairie Pothole Region. During wetland visits we also evaluated upland land-use surrounding wetlands. Later, we measured water surface area of wetlands from 2003–2010, delineated wetland catchments, and estimated the area of wetlands historically drained within catchments of our focal wetlands using remote-sensing techniques. We classified climate conditions relevant to wetland hydrology during 2003–2010 using a spatially explicit standardized precipitation–evapotranspiration index. The resulting classification was 1) 2003–2005 as a wet period; 2) 2006–2008 as a dry period; and 3) 2009–2010 as a wet period. We evaluated water surface area dynamics within wetlands by calculating the intrinsic rate of wetland growth during each the drying and wetting phase of the 2003–2010 climate cycle—a phase is a transitional change between periods. Analysis of the rate of wetland growth indicated that wetlands in catchments with more historic wetland drainage increased in surface area more during the wetting phase than they reduced during the drawdown of the preceding drying phase. These rates suggest that in highly modified catchments wetlands that have not yet filled their topographic basin are likely to continue to increase until they reach a basin spill point elevation.

We compared depth measurements taken in 2004–2005 from a previous study to our depth

measurements. We found wetland water depth increased 0.66 m (SD = 0.76) and 0.35 m (SD = 0.43) between 2004–2005 to 2010 and from 2010 to 2011, respectively. Corresponding to the increase in depth of wetlands, we observed greater occurrence and abundance of fish in wetlands than previous reports. In 2011, we captured fathead minnows (*Pimephales promelas*) and fish of any type in 45% and 60% of wetlands sampled, respectively. This represents a 13% and 12% increase from occurrence in 2004–2005, respectively. Where water depth increased less, we observed greater coverage of the wetland by cattail. This is consistent with other reports of stabilization of water-level is favorable to cattail abundance. Our results suggest that water-level increases in highly modified catchments coupled with stabilization after wetlands reach a basin spill elevation could create conditions suitable for both fish and cattail to become abundant and maintain stable or invasive populations.

We attempted to uncouple influences of climate variability and landscape modifications on changes of amphipod densities. While, regional-mean amphipod densities in 2010–2011 were similar to those reported from 2004–2005, densities did change within each wetland. We found evidence that high levels of historic wetland drainage within catchments of remaining wetlands negatively impacted densities of both *Hyalella azteca* and *Gammarus lacustris*. We also found evidence that water-level drawdown had a negative impact on *Hyalella azteca* densities.

Drainage of wetlands within catchments has increased surface area of remaining wetlands that receive drainage water, and we suspect wetland drainage is likely to have had deleterious effects on amphipod populations. Our data suggests that 39% of wetlands receive enough consolidation drainage water to unbalance water budgets within climate cycles enough to cause wetlands to ultimately increase in size to a point in which they become connected to adjacent wetlands and maintain stable water-levels. We suspect that this ultimately shifts these wetlands into a sustained lake phase (or “open-water” phase) which may persist until either an extreme-sustained drought event or conservation actions occur to restore upper-catchment wetlands. Semipermanent wetlands historically interacted within a complex of wetlands of various hydroperiods that mostly lacked surface connection, thus these wetlands fluctuated in water-level in response climate variability at different temporal rates. These complexes of interacting wetlands are potentially an integral facet of the region’s ability to support waterbird populations throughout climate cycles. Where wetlands are consolidated within modified uplands, restoration of wetland complexes of various hydroperiods could prevent further degradation of wetland productivity in the region and could cumulatively improve productivity realized at a regional scale.

## **Introduction**

Prairie pothole wetlands provide critical migration and breeding habitat for numerous waterfowl and other waterbirds, including fourteen North Dakota Comprehensive Wildlife Conservation Strategy

Level-I and Level-II Species of Conservation Priority (NDGF 2004). Effective management and restoration of wetland habitats targeted to species of conservation priority relies on understanding how drainage and consolidation of wetlands and upland disturbances ultimately influence productivity in wetlands, and also how they might interact with wet–dry climate cycles to influence inter-annual hydrologic dynamics of wetlands. Aquatic invertebrates are an important component of prairie wetland communities and productivity (Euliss et al. 1999), and agricultural landscape modifications have been linked to declines or shifts in aquatic invertebrates (Euliss and Mushet 1999; Anteau et al. 2011).

Productivity of prairie wetlands has been thought to be primarily driven by inter-annual hydrologic fluctuations (i.e., wet-dry cycles; Euliss et al. 1999). The drying of wetlands or portions of wetlands allows for nutrient cycling and a subsequent pulse of productivity after wet conditions return (Euliss et al. 1999). Similarly, wetlands likely receive increases in nutrients whenever uplands are inundated. These hydrologic fluctuations are driven by climate variability and shape floral and faunal community structures of Prairie Pothole Region (PPR) wetlands (Kantrud et al. 1989). Native communities in prairie pothole wetlands are adapted to the dynamic nature of these systems. Accordingly, changes in hydrologic fluctuations as a result of changes in climate cycles represent a threat to native communities and productivity of prairie pothole wetlands. Moreover, abundance and quality of PPR wetlands has declined due to landscape modifications, primarily related to agriculture (Dahl 1990; Anteau and Afton 2008; Bartzen et al. 2010; Anteau and Afton 2011). Tillage within a catchment can increase hydroperiod dynamics of less-permanent wetlands, but historically has had less of an effect on more-permanent wetlands that primarily receive water input from groundwater (Euliss and Mushet 1996). However, landscape modifications, such as draining smaller, less-permanent wetlands into larger, more-permanent wetlands (i.e., consolidation drainage), threaten native communities and productivity by increasing surface connections among remaining more-permanent wetlands and disrupting hydrologic fluctuations of prairie pothole wetlands in response to climate cycles (Merkey 2006; Anteau 2012). Therefore, effects of landscape modifications on wetland hydrology could threaten native communities and wetland productivity.

Consolidation drainage is a common practice throughout the PPR and increases connectivity among the remaining more-permanent basins through drainage ditches and tile (Anteau 2012; McCauley et al. 2014). In contrast, natural surface connections between basins occur only during high water periods of wet cycles. Less storage in the upper watershed and increased connections among wetlands as a result of drainage may produce high and stable water regimes in remaining wetlands (Anteau 2012; McCauley et al. 2014). Therefore, understanding relationships between inter-annual hydrologic dynamics and landscape modifications is a prerequisite step to modeling the effects of climate and land-use change on the hydrologic function and productivity of prairie wetlands.

In this report we have attempted to consistently use the following terms regarding the wetland setting, and have provide our definitions here. A focal wetland is semipermanent or permanent lacustrine wetland that was randomly selected for the current study. The wetland catchment is the portion of the landscape in which surface water flows into a focal wetland, and catchments may include more-intermittent wetlands and their catchments if those wetlands would spill into the focal wetland once they have filled their basin (McCauley and Anteau 2014). A wetland basin is the topographic depression that collects surface water that which is isolated from basins of other wetlands of an equal or more permanent hydroperiod.

Semipermanent wetlands are larger, more-permanent wetlands that hold water during most years excluding those during extreme droughts. These wetlands are capable of producing high levels of food resources that support a variety of higher level consumers (e.g., waterbirds, salamanders, and fish; Kantrud and Stewart 1984; Batt et al. 1989; Kantrud et al. 1989; Euliss et al. 1999; Anteau and Afton 2009a; Anteau 2012). Water levels in semipermanent wetlands fluctuate in response to inter-annual variability of precipitation that falls on the catchment; however, during short-term drought periods water levels of more-permanent wetlands might drawdown less than less-permanent wetlands because more-permanent wetlands likely have more interactions with groundwater (Euliss and Mushet 1996). Prairie pothole wetlands in a watershed are part of a hydrologic network that exists through groundwater connections (LaBaugh et al. 1987; Winter and Rosenberry 1995). Semipermanent wetlands are primarily flow-through or discharge wetlands that receive groundwater; however, at times they also recharge groundwater (LaBaugh et al. 1987; Kantrud et al. 1989; Euliss et al. 2004). Wetlands in the PPR historically were isolated, lacking surface connections to other basins, except during peak years of major wet cycles when high water levels create surface connections between wetland basins (Leibowitz and Vining 2003). These connections serve as natural corridors of dispersion for water-obligate species (e.g., fish). Evaporation and evapotranspiration are the primary causes of water loss and when water levels recede during drying periods these wetlands again become isolated (Shjeflo 1994; Leibowitz and Vining 2003; Tiner 2003). Waterbirds may become dependent on the productivity of more-permanent wetlands during dry years when these basins are the only wetlands that hold surface water (Niemuth et al. 2006; Anteau 2012). It is necessary for waterbird conservation to understand the influence of climate variability on fluctuations of productivity in these more-permanent wetlands because in dry years they may be the only suitable habitat for waterbirds in the region and during wet years these wetlands are capable of producing great amounts of food resources. Furthermore, there are many vertebrate species of conservation importance that specialize in these habitats (e.g., tiger salamanders [*Ambystoma mavortium*], lesser scaup [*Aythya affinis*], canvasback [*Aythya valisineria*], redhead [*Aythya americana*], black terns [*Chlidonias niger*], and pied-billed grebe [*Podilymbus podiceps*]; Kantrud and Stewart 1977,

1984; Kantrud et al. 1989; Anteau and Afton 2009a).

In prairie wetlands, density of amphipods can serve as an indicator of wetland and water quality because amphipods are sensitive to contaminants, disturbances in uplands, and invasive species (Grue et al. 1988; Tome et al. 1995; Duan et al. 2000; Anteau and Afton 2008; Hentges and Stewart 2010; Anteau et al. 2011). In 2004–2005, amphipod density was low across the PPR (including North Dakota) compared to historical records (Anteau and Afton 2008), perhaps due to landscape modifications (Anteau and Afton 2008; Anteau et al. 2011). However, most of the region in years before 2004 and 2005 experienced a regime of relatively high and stable water since 1993; therefore, amphipod numbers could have been low due to a period of little inter-annual water-level variation (Euliss et al. 1999; Euliss et al. 2004). Many parts of the PPR in North Dakota experienced moderate to severe drought during 2006–2008 (Figure 1; NCDC 2014), making it possible for basins to have lower water levels and subsequent nutrient cycling (Euliss et al. 1999). In spring 2009, wet conditions returned for most prairie wetlands in North Dakota (Figure 1; NCDC 2014). Thus, comparing water level data and amphipod densities collected in 2010 and 2011 to those collected in 2004 and 2005 should provide, 1) an estimate of the number of amphipods available for spring migrating and pre-breeding waterbirds under climate conditions expected to be more ideal for amphipod production, 2) the ability to uncouple and understand the influences of hydrologic regime and landscape modifications upon amphipod density, and 3) an ability to examine how landscape modification influences the effect of inter-annual variation of climate on hydrology and amphipod density and ultimately wetland productivity.

Changes in hydrologic dynamics and wetland connectivity have the potential to influence ecological communities in prairie wetlands. High-stable water regimes may shift community species composition toward those adapted to more stable environments. Further, increased connectivity among basins would provide colonization corridors for aquatic-obligate species (e.g., fish) that rarely colonize isolated basins (Peterka 1989). Together these conditions could favor certain species (e.g., fish and cattail [*Typha* spp.]) to become invasive and further threaten natural functions of prairie wetlands; those species were historically kept in check in native communities by dynamics and isolation of wetlands (Shay et al. 1999). The prevalence of fish and cattails found in prairie wetlands in 2004 and 2005, at the start of a drying phase following a high-stable water regime, apparently increased compared to historical record (Swanson 1992; Anteau and Afton 2008), which has implications for habitat structure and abundance and quality of forage for waterbirds. Therefore, it also is important to understand how landscape modifications have influenced the abundance and distribution of fish and cattail in prairie wetlands of North Dakota.

Conservation programs that protect and provide upland-nesting habitat and wetland habitat for breeding waterfowl and other waterbirds (e.g., Conservation Reserve Program and Wetland Reserve

Program, U.S. Department of Agriculture; and Wetland and Grassland Easements, U.S. Fish and Wildlife Service, Department of the Interior) have been periodically updated with research to optimize effectiveness of conservation activities (e.g., Niemuth et al. 2009). However, programs that protect and restore wetland habitats generally have not been updated because there is a lack of understanding of complex processes and functions of these wetlands (Knutsen and Euliss 2001). For example, restoration projects often are focused on restoring hydroperiods (i.e., water holding capacity and duration) by plugging drainage ditches or removing tile. However, these efforts applied to individual wetlands often result in wetlands that have different hydroperiods than that expected of natural wetlands in the same setting (Galatowitsch and van der Valk 1994, 1996). Perhaps restoring wetland complexes composed of wetlands with various hydroperiods can more closely mirror the natural hydrologic function of all wetlands within the complex (Galatowitsch and van der Valk 1994). Because most wetlands of the PPR exist in a highly modified landscape, much more research is required to better structure these programs to restore ecosystem function and improve or restore productivity. Furthermore, it is important to provide information to managers about drivers of productivity and function in wetlands in relation to natural and anthropogenic influences. Moreover, this information should be useful for setting targets and goals used in conservation and restoration of wetland habitats for waterbirds, including species of conservation priority. Specifically, this essential information includes 1) an understanding of how drainage and consolidation of wetlands and upland disturbances influence productivity in remaining wetlands, 2) how those disturbances might interact with inter-annual hydrologic dynamics of wetlands, and 3) a basis for modeling hydrologic and productivity changes of wetlands in relation to climate change forecasts. Our results in the context of those from earlier studies (Anteau and Afton 2008) provide insight into drivers of wetland productivity on the modified landscape of the PPR. Conservation planning will benefit from a better understanding of mechanisms that affect forage availability for waterbirds that must acquire nutrient reserves while migrating through North Dakota in spring and for waterbirds that breed in North Dakota (i.e., mechanisms of the spring condition hypothesis; Anteau and Afton 2004, 2009b).

### **Objectives**

- 1) Examine changes in depth and open-water surface area of semipermanent and permanent wetlands of North Dakota in relation to climate, upland disturbance, and wetland connectivity.
- 2) Examine changes in amphipod densities in semipermanent and permanent wetlands of North Dakota in relation to water-level change and landscape modification.
- 3) Examine the occurrence and abundance of fish in semipermanent and permanent wetlands of North Dakota in relation to water-level change and wetland connectivity.

- 4) Examine proportions of cattail in emergent vegetation and coverage of wetland area by cattail in semipermanent and permanent wetlands of North Dakota in relation to water-level change and upland disturbance.

## **Methods**

### **Study Area**

Our study area included the Missouri Coteau, Northern Glaciated Plains, and Red River Valley eco-physiographic regions of North Dakota (hereafter regions; Figure 2). In 2010 and 2011, we returned to 140 lacustrine semipermanent and shallow-water permanent wetlands that Anteau and Afton (2008) surveyed once in either 2004 or 2005 (Table 1). Wetlands were randomly selected by Anteau and Afton (2008) using the following design that resulted in 154 wetlands sampled across the three regions in North Dakota. Deviation from the expected number of wetlands sampled based on the design can be accounted for as follows, we did not sample three wetlands that became incorporated into the flooded Devils Lake, we were unable to get permission to access seven wetlands among all regions, we did not sample one wetland due to uncertainty of wetland location, and we did not sample wetlands of the RRV region that were in Minnesota. Anteau and Afton (2008) selected wetlands from candidate townships that had at least 200 ha of semipermanent wetlands (National Wetland Inventory data [NWI], U.S. Fish and Wildlife Service). Regions were divided into three sub-regions based on latitude ( $<47^{\circ}\text{N}$ ,  $47\text{--}48^{\circ}\text{N}$ ,  $>48^{\circ}\text{N}$ ). Sub-region size and number of candidate townships were used to allocate the number of sampling clusters within each sub-region; two, four, and one clusters were assigned to each sub-region, or 6, 12, 2 clusters total, in COT, NGP, and RRV, respectively. The mid-latitude RRV sub-region did not have an assigned cluster because there were no candidate townships in North Dakota portion of this sub-region. Each sampling cluster was comprised of three randomly selected 36-square-mile townships (27,972 ha total). The centers of the second and third townships selected were constrained to within 50 km of the center of the first randomly selected township. Three randomly selected semipermanent or permanent wetlands ( $>4$  ha) were selected in each township. Semipermanent wetlands composed 59%, 72%, 50% of the sample in COT, NGP, RRV, respectively. Wetlands must have had an open water area larger than 120 m across to be sampled in 2004 or 2005. In 2004 or 2005, if reselection of a wetland in the field was necessary, the nearest suitable semipermanent wetland was sampled. Anteau and Afton (2008) ultimately did not sample three wetlands in some townships due to difficulties accessing private land and finding suitable replacement wetlands within the township.

### **Spring Wetland Surveys**

In April and May of each year 2010 and 2011, we resurveyed 140 and 131, respectively, randomly selected lacustrine semipermanent wetlands and shallow-water permanent wetlands (i.e.,



shallow lakes) that were initially surveyed at the same time of year in either 2004 or 2005 by Anteau and Afton (2008). We surveyed wetlands using techniques described in Anteau and Afton (2008) to collect data on aquatic invertebrate density, fish abundance, water quality, and generalized wetland vegetation structure. Data were collected on randomly located transects extending from shoreline toward the center of the wetland (see Figure 3). We georeferenced all sampling locations in the field using geographic information system (GIS) data loggers (Trimble GeoXT, Trimble Navigation, Sunnyvale, CA).

**Water depth.**-To estimate change in depth among surveys of 2004 or 2005 (Anteau and Afton 2008) and surveys of 2010 and 2011, we measured water depth ( $\pm 0.1$  m) at 10 locations estimated to be 10 m into open water from 2004 or 2005 the shoreline or emergent vegetation to open-water interface. When waves were present, the average depth between wave crests and troughs was recorded. Prior to field work, we delineated the shoreline or emergent vegetation to open-water interface of each wetland using imagery (National Agricultural Imagery Program, U.S. Department of Agriculture; hereafter NAIP) acquired in the summer (July) prior to each spring survey by Anteau and Afton (2008). We used the imagery from the previous year because it better represents the location of the emergent vegetation to open-water interface that Anteau and Afton (2008) used to locate their sampling locations. The interface was digitized by using GIS software at a scale of 1:5,000. We offset (buffered) the digitized interface 10 m toward the center of the open-water wetland polygon to approximate 2004 or 2005 sampling locations. We derived our 10 random points from the 10-m buffer, but we constrained point locations so there is a minimum distance of 40 m between points. We loaded the random points onto the Trimble GeoXT to navigate to sampling locations. Sample locations found within the emergent vegetation ring were recorded as such, because different dynamics of sedimentation and accumulation of organics were expected. Additionally, in 2011, we measured depth at four georeferenced locations where 10-m depth sampling occurred in 2010 (see Figure 3).

**Amphipod densities.**-We sampled amphipods in open water using a D-shaped sweep net (1,200  $\mu\text{m}$  mesh, 0.072  $\text{m}^2$  opening, WARD'S Natural Science, Rochester, NY) at four amphipod-sampling transects (hereafter primary transects; Figure 3). Sampling stations at each transect were located at 10 and 60 m from the shoreline or emergent vegetation to open-water interface. Sample locations were adjusted along transects to ensure the station depth is between 0.5 and 3 m (see Anteau and Afton 2008). Depth at each sampling station was recorded to the nearest 0.1 m. At each station, we sampled invertebrates using a sweep-net; each sample consisted of a sweep across the bottom for a distance equal to the water depth, and a sweep up through the water column. We calculated the volume of water sampled (VS;  $\text{m}^3$ ) with a sweep net using the following equation (Anteau and Afton 2008):

$$VS = 2(\sum D_i) \times SN,$$

where  $D_i$  = depth at each sampling location and SN = area of the sweep-net opening (0.072  $\text{m}^2$ ).

Vegetation or debris that was brought up in the sweep-net was included in the sample, unless >50% of the object hangs outside the net. We composited the samples into 10- and 60-m samples for each wetland, and samples were chilled with ice then frozen within 8 hours of collection. In the laboratory, we allowed the samples to thaw, and then we sorted and counted amphipods by species.

**Wetland habitat.**-Emergent vegetation ring width (0, 1–4, 5–10, 11–30, 31–60, or >60m), proportion ( $\pm 0.1$ ) of emergent vegetation that is cattail, bulrush, or other emergent vegetation, width of upland buffer (0, 1-4, 5-10, 11-50, >50m), and immediate upland land-use (up to 100m; native grassland, restored grassland, unknown grassland, shrubs, trees, hayland, cropland, developed; Table 2) were characterized at all four primary transects and six additional randomly selected transects (hereafter secondary transects; Figure 3). In our analyses we used the midpoint of categorical estimates with the maximum value of 90 m for emergent vegetation ring width and maximum value 75 m for width of upland buffer.

**Fish communities.**-In 2010, we experimented with using a mini-Missouri benthic trawl (Herzog et al. 2009; Sherfy et al. 2009) to sample wetland fish and salamander communities. If successful, this effort alone would have provided the necessary data to describe various taxa of wetland fish communities, eliminating the need for return trips to wetlands that minnow traps and gill nets require. Additionally, we planned to use minnow traps in one randomly selected wetland of each township sampled (i.e., one-third of the wetlands). We planned to rely on the mini-Missouri trawl effort to adequately sample fish communities in all wetlands and planned to use data from the minnow traps to correspond to data collected by Anteau and Afton (2008). Unfortunately, trawls did not perform well in wetland habitats in 2010; our catch rates were very low, and often trawls did not catch fish in wetlands where fish were caught in minnow traps. In response to difficulties catching fish with the mini-Missouri trawl, we proceeded to place minnow traps in all remaining wetlands (75% total). We did not obtain adequate data for fish communities in wetlands for 2010, therefore our analyses relied primarily on fish data collected in 2011.

In 2011, we used minnow traps and an experimental gill net in every wetland (see Anteau and Afton 2008). We used Gee-style minnow traps; we set five traps with 6.35 mm mesh and 2 with 3.175 mm mesh at the emergent vegetation to open-water interface (or equivalent position from the shoreline if no emergent vegetation is present) at seven transects (Figure 3). The monofilament experimental gill net (21  $\times$  2 m with seven 3-m panels ranging in mesh size from 1.9–7.6 cm) was set at a transect perpendicular to the shoreline with the small mesh end of the net at the emergent vegetation to open-water interface (or equivalent position from the shoreline if no emergent vegetation is present). Minnow traps and the gill net were deployed for 12–24 hours including an overnight period. At the time of trap and gill net retrieval, we sorted and counted fish by species and by length category (<5, 5–10, 10–20, 20–40, >40

cm). We counted each salamander and measured their body length to the nearest cm. We took digital photographs of any animals we are unable to identify in the field, and later identified them in the office using keys and field guides. After identifying and measuring the fish and salamanders, we immediately returned healthy fish to the water, resuscitated exhausted individuals in the water by moving water over the gills, euthanized severely injured animals (in accordance with animal care and use protocol), and punctured the swim bladder of fish found dead in traps or gill net and returned them to the water.

We classified all captures into one of four categories: fathead minnows (*Pimephales promelas*), other small fish species typically <10 cm (e.g., other minnows [Cyprinidae], darters [Anhingidae], and sticklebacks [Gasterosteidae]), large fish species typically >10 cm (e.g. northern pike [*Esox lucius*], walleye [*Sander vitreus*], yellow perch [*Perca flavescens*], sunfishes [*Lepomis* spp.], and bullhead and catfish [Ictaluridae]), and salamanders. We calculated catch per unit effort (relative abundance) for each gear type by dividing the number of captures of each class by the hours the gear was in the water. For each class, we summed the quotients of the two gear types.

**Wetland setting.**-We classified current agricultural impacts surrounding (up to 400 m) each wetland using ground observations in 2010 and 2011. Land-cover data were collected using GIS software in the field. We attributed empty polygon outlines of land-cover data (Habitat and Population Evaluation Team 1996) based on current observations with one of the following categories: native grassland, restored grassland, unknown grassland, hayland, cropland, shrubs, trees, developed, barren, or wetland. We calculated the proportion of cropland for the upland area that was both within the defined catchment (see above) and within 400 m of the subject wetland. We recorded presence/absence of any surface water connections leading to or from the focal wetland, including: inflow and outflow streams, drainage ditches, culverts, road ditches, and temporal overland connections between wetland basins.

### **Remote Sensing**

**Climate index.**-We used a fine-scale climatic wetland hydrologic index (~3 km pixel) in our analysis of wetland surface area change because climate conditions can vary across North Dakota. The index was derived by Post van der Burg et al. (2014) to estimate the effect of climate on water surface area of wetlands using the catchment size of the wetland and standardized precipitation-evapotranspiration index calculated from PRISM (Parameter-elevation Regression on Independent Slopes Model) Climate Group data (PRISM Climate Group 2002). The temporal summary of the index that best explained water levels, and used here, incorporated climate conditions over the previous 10 years with a triangular-decay-temporal-weighting function (Post van der Berg et al. 2014). Index values above zero represent hydrologic wet conditions and values below zero represent hydrologic dry conditions.

Based on climate conditions (Figure 4), we classified 2003–2005 as a wet period, 2006–2008 as a dry period, and 2009–2010 as a wet period. We then identified the drying phase as the change between

the first wet period and the dry period, and the wetting phase as the change between the dry period and the second wet period. We structured our analysis of wetland surface area change by these two climate phases. We calculated the change in climate index for each climate phase as the difference in the index value between the year with the maximum surface area and minimum surface. In our model, we controlled for spatial variability in climate by using the difference of the change in climate index for each phase from the mean change in climate index for that phase. The resulting value then represents any deviation in magnitude of climate dynamics from the mean for each phase, thereby accounting for spatial variability in climate within each phase.

**Water surface area.**-We delineated water surface area of each sampled wetland by photointerpretation of National Agriculture Imagery Program (NAIP; U.S. Department of Agriculture) areal imagery for 2003–2006 and 2009–2010. Photointerpretation was performed while images were viewed as panchromatic instead of true-color, because they were done as part of a larger study that involved some panchromatic imagery (see McCauley et al. 2014). Where the waterline was obscured by emergent vegetation, we approximated the waterline to be halfway between the emergent-vegetation to open-water interface and clearly identifiable upland. NAIP imagery was not available for 2007 and 2008. For those years we delineated the wetland water surface area once in either 2007 or 2008 using high-resolution digital elevation model (DEM; source data: 1 m pixel LiDAR; Data available from the U.S. Geological Survey) or ~1.25 m pixel interferometric synthetic aperture radar (IfSAR) orthorectified image (Intermap Technologies, Inc., Englewood, Colorado).

We calculated the intrinsic rate of wetland growth for each climate phase as the natural logarithm ( $\ln$ ) of the quotient from the final surface area divided by the initial surface area. Within this calculation we used the maximum surface area from the wet period and the minimum surface area from the dry period. The intrinsic rate of increase (wetland growth) was useful as a response variable in our model to accommodate the complexities of evaluating dynamics in a time series, such as it is useful in population biology (Hastings 1997).

**Catchments.**-Catchments were derived for each of the sampled wetlands using high resolution DEMs (3 m pixel LiDAR or 5 m pixel IfSAR) and surface hydrology modeling tools by McCauley and Anteau (2014). We truncated some catchments (46%) that were large or highly irregular in shape to a 2.5 km maximum radius from the wetland basin for logistical reasons associated with assembling landscape variables, such as amount of wetland area drained. The 2.5-km radius encompassed >90% of the total catchment area for 68% of catchments. Landscape conditions within these 2.5-km truncated catchments should represent the condition of the full catchment, and the conditions nearest the wetland basin likely influence the basin most. Therefore, we assume the 2.5-km-truncated catchment provided a reasonable area to evaluate impacts of land use on wetlands within our study and are an improvement over the simply

buffering around a wetland a set distance, which is a common practice (McCauley and Anteau 2014).

**Catchment drainage.**-We estimated the percent of the catchment area that was drained wetland prior to 2010 using multiple data sources, including: aerial photographs, DEM, NWI, and spatially explicit soil data (see McCauley et al. 2014). These same data sources that were available from years prior to 2010 were used to identify evidence of drain installation back to 2003. Wetlands were identified as drained if they were present in historical photographs (dating back to 1937) but not present in current photographs, or if the wetlands were identified as part of a drainage network. Significant drainage occurred prior to 2003 in our study area; however, we found negligible evidence of additional drainage after 2003.

**Basin area.**-We measured the basin area to determine the maximum water surface area of a wetland that the basin could hold before the water would spill and flow out of the basin. We used the high-resolution DEMs (3 m pixel LiDAR or 5 m pixel IfSAR) to find the spill point of the basin and then delineated the area at that spill point elevation within the basin. We predicted that wetlands in basins that were near full or that were full would have less surface area and depth dynamics. Further, the proportion of the basin that focal wetland filled likely is an index of potential connectivity because surface water connections are typically at higher elevations within the basin. Therefore, we calculated the proportion of the basin that the focal wetland filled at the start of each climate phase.

**Bank Slope.**-We calculated the bank slope of each wetland because we expected water-volume-to-surface area relationships to differ with varying bank slopes. Wetlands with steeper sides would have a smaller change in surface area with added volume than wetlands with flatter sides. Using the high-resolution DEMs, we recorded the average elevation of the water surface for all wetlands in 2007 or 2008 (the driest years) and in 2010 (a wet year). We calculated bank slope of the wetland using the equation

$$\frac{Depth_{wet} - Depth_{dry}}{\sqrt{\frac{Area_{wet}}{\pi}} - \sqrt{\frac{Area_{dry}}{\pi}}}$$

On average, 2010 was a wetter year and water levels were higher than in 2007 or 2008 but in those cases where 2010 water levels were actually lower than in 2007 or 2008, another wetter year was substituted.

**Soil characteristics.**-We used soil survey data from the USDA Soil Survey Geographic Database (SSURGO) to evaluate the potential impact of soil fertility on wetland productivity. For each wetland catchment we calculated areal-weighted means down to 20 cm depth for quantity of carbonate as  $\text{CaCO}_3$  and percent composition of each silt and organic material. We suspect that quantity of carbonates as  $\text{CaCO}_3$  in surrounding upland soils is tied to alkaline waters being more suitable for amphipod survival (Stephenson and Mackie 1986) and general dietary calcium requirements of crustaceans (Pennings et al. 2000). Silt and organic material are associated with fertile soils. We combined the two characteristics in

a principal component analysis and used the first component to index soil fertility. Land use for crop production and wetland productivity are both likely correlated with soil fertility. Accordingly, in our analyses of change in amphipod density we adjusted land use to the suitability of soil for cropland by using the residual from percent cropland surrounding a wetland regressed on the first component of the fertile soil index.

### **Statistical Analyses**

***Change in surface area.***-We calculated regional means for change in water surface area from the 2003–2005 wet period to the 2009–2010 wet period. We included randomly selected wetlands and selected three Cottonwood Study Area wetlands that had complete series of delineated water surface areas in this analysis. We used the maximum surface area observed during each period, and subtracted the surface area of the earlier period from the most recent period. We used analysis of covariance to evaluate change in surface area by region as a fixed effect and controlling sampled township as a random effect (lme4 package in Program R; R Development Core Team 2010; Bates et al. 2011). We calculated 95% confidence intervals for regional means.

To better understand variability in water surface area dynamics related to landscape modification we evaluated the effect of historic drainage of wetlands within catchments of focal wetlands on water surface area increases of focal wetlands. We included wetlands that had complete field and remotely sensed data in this analysis. We evaluated the effect (i.e., drainage-by-climate phase) on the intrinsic rate of wetland growth using mixed-effects regression models (lme4 package in Program R; R Development Core Team 2010; Bates et al. 2011); we included the following covariates: logit transformed basin-full, catchment drainage-by-basin-full interaction, percent cropland, maximum observed depth, bank slope (*ln*), change in climate index, and catchment area (*ln*). Furthermore, we included an interaction of each covariate by climate phase because we expected the rate of increase response to be of opposite sign between climate phases. We used a wetland identifier as a random error term to structure the analysis as a repeated measure.

We conducted selection of covariates by comparing a one-variable-removed reduced model to the full model (Arnold 2010; Lachish et al. 2013). We repeated this process for each of the fixed-effect covariates. For each interaction with climate phase tested, we removed the interaction term, and then removed the interaction term and main effect in separate reduced models. We evaluate if the removed covariate was informative using Akaike's Information Criterion adjusted for small sample size ( $AIC_c$ ; Burnham and Anderson 2002). When the reduced model  $AIC_c$  was increased  $\geq 2$  points for each estimated parameter (K) removed, we included the removed covariate in the final model (Arnold 2010; Lachish et al. 2013). We compared the final model to a null model using  $AIC_c$  to determine model adequacy (Burnham and Anderson 2002). We predicted rates of water surface area increase at a

combination of low, moderate, and high levels of both catchment drainage and percent basin filled by the focal wetland. Prediction levels were created by slicing the data into thirds for each factor and using the mean value from each one-third level of the two factors. We held all other covariates at mean levels. We calculated 85% confidence intervals of these predictions, a criterion of parameter-evaluation that is similar to variable-selection criteria used (Arnold 2010).

***Change in water depth.***-We calculated mean regional changes in water depth from the earlier sampling period of 2004 or 2005 to the recent sampling period in 2010 and for the change between 2010 to 2011. We calculated mean depth of the wetlands during 2004 or 2005 by averaging the four measurements at 10-m sweep-net sampling locations. We calculated mean depth of the wetlands during 2010 and 2011 by averaging the 10 depth measurements taken at the estimated location of the 2004 or 2005 10-m sampling location. We calculated the change in depth by subtracting the 2004 or 2005 depth from that measured in 2010 and subtracting 2010 depth from that measured in 2011. We examined change in water depth across sampling periods (i.e., 2004 or 2005 to 2010) by region as a fixed effect, and controlling sampled township as a random effect within an analysis of covariance (lme4 package in Program R; R Development Core Team 2010; Bates et al. 2011). We conducted a second identical analysis for change in depth within the second wet period (2010 vs. 2011). We calculated 95% confidence intervals for regional means.

To better understand variability in depth change through the climate cycle we evaluate the effect of landscape and climate factors. We included wetlands that had complete field and remotely sensed data in this analysis. We calculated the change in depth from the initial sampling in 2004 or 2005 to the depth of the final sampling in 2011. We constructed mixed-effects regression models (lme4 package in Program R; R Development Core Team 2010; Bates et al. 2011) to evaluate the effect of change in climate index between wet periods, catchment area (*ln*), percent basin-full, catchment drainage, percent cropland, presence/absence of surface connections, bank slope (*ln*). We included a catchment drainage-by-basin-full interaction term because we expected reduced depth increases for wetlands that nearly filled their basins within in catchments with high amount of drainage compared to greater increases in depth in wetlands that were less full yet also in catchments with high amounts of drainage. We also included a catchment area-by-change in climate index interaction term because we expected larger catchments to collect more volume of precipitation in wetter conditions than smaller catchments. We included the sampled township as a random error term. We selected variables for the final model using the same one-variable-removed reduced model comparison to the full model method that was described in the surface area analysis (Arnold 2010; Lachish et al. 2013).

***Amphipod abundance.***-We calculated densities of amphipods (count per cubic meter of water) for *Gammarus lacustris* (hereafter *Gammarus*) and *Hyaella azteca* (hereafter *Hyaella*), and *Gammarus*

and *Hyalella* combined in each randomly selected wetlands sampled in 2004 or 2005 and in 2010 and 2011. For each amphipod class, we compared densities among regions in separate analyses of variance (PROC MIXED; SAS Institute 2002). Because amphipod densities followed a skewed-right distribution, we  $\ln(+1)$ -transformed densities to meet assumptions of normality (Devore 2000); we report back-transformed geometric least-squares means.

We calculated mean change in amphipod density for landscape modifications and water-level fluctuation effects using an analysis of variance. For each *Gammarus* and *Hyalella*, we calculated the change in density by subtracting the 2004/05 density from both the 2010 and 2011 density. We then  $\ln$ -transformed the absolute value of the difference (+1) and then applied the original sign to the  $\ln$ -transformed value. We calculated the wetland area exposed during drawdown of the drying phase and wetland area flooded during the wetting phase using the equation:  $SA_{\max} - SA_{\min}$ ; where SA is observed surface area in hectares. For the drawdown calculation, we used the maximum surface area from 2003–2005 and the minimum from 2006–2008. In the flooding calculation we used the surface area observed in 2009 for spring 2010  $SA_{\max}$  and the maximum in 2009–2010 for spring 2011  $SA_{\max}$ , and we used the minimum from 2006–2008. We classified wetlands into either low, moderate, and high levels for each 1) percent catchment area that was drained wetland, 2) focal wetland area exposed during the drying phase, and 3) focal wetland area flooded during the wetting phase of the climate cycle. We defined levels using one-third breaks within the sampled distribution of each of the three factors. We report back-transformed means and 95% confidence intervals.

***Fish occurrence and abundance.***-We calculated the percent of wetlands in which we captured fathead minnows, small fish, and large fish, and fish of any group to evaluate fish occurrence between sampling periods of 2004 or 2005, and 2011. We used a mixed-effect linear model to calculate mean abundance during each sampling period by using catch per unit effort ( $\ln + 1$ ) as a relative abundance index and account for township sampled as a random effect (lme4 package in Program R; R Development Core Team 2010; Bates et al. 2011). We report back-transformed geometric means with calculated 95% confidence intervals. In separate mixed-effect models for fathead minnows and fish of any group, we evaluated the effect of catchment drainage and percent the focal wetland filled its topographic basin on abundance in a repeated measure analyses for wetlands sampled in 2004 or 2005 and 2011 while accounting of sampled township as a random effect (lme4 package in Program R; R Development Core Team 2010; Bates et al. 2011). We predicted abundance (i.e., catch per unit effort) for fathead minnows and fish of any group for low, moderate, and high levels of both catchment drainage and percent basin filled by focal wetland. Prediction levels were created by slicing the data into thirds for each factor and using the mean from value from each level, and we calculated 95% confidence intervals.

***Cattail abundance.***-Within the emergent vegetation ring around wetlands, cattail generally is



contiguous and other emergent vegetation species generally are on the outer or inner edge of the ring (M. Anteau and M. Wiltermuth, *pers. obs.*); therefore, we calculated the width of the ring that is cattail by multiplying the midpoint of the emergent vegetation ring width category and the proportion of the ring that was cattail. If the >60-m category was recorded, we set a value of 90 m. We then averaged these adjusted midpoint width values of all 10 measurements within each wetland. Our analyses included wetlands that were visited in 2004 or 2005, 2010, and 2011, and that had estimates of wetland drainage within their catchments. We estimated the proportion of the wetland area covered by cattail in each region while controlling for sample township as a random effect using a mixed effect regression model (lme4 package in Program R; R Development Core Team 2010; Bates et al. 2011). We also evaluated the effect of catchment drainage and change in water depth on proportion coverage of each major emergent vegetation type while controlling for wetland area (*ln*) as a fixed effect and sample township as a random effect (lme4 package in Program R; R Development Core Team 2010; Bates et al. 2011). We ran separate mixed models for cattail, bulrush, and “other” species. We predicted coverage by each emergent vegetation group for low, moderate, and high levels of both catchment drainage and change in wetland depth by slicing the data into thirds for each factor and using the mean from value from each one-third level, and we calculated 95% confidence intervals.

## **Results**

### **Climate Index**

Mean climatic wetland hydrologic index was 0.3448 ( $\pm 0.0242$  SE), -0.3912 ( $\pm 0.0304$  SE), 0.5845 ( $\pm 0.0289$  SE), for 2003–2005, 2006–2008, and 2009–2010, respectively (Figure 4). The index was different from zero in all periods and different from each other in all periods.

### **Wetland Surface Area**

We evaluated water surface area change in 147 wetlands. Change in surface area from the 2003–2005 wet period to the 2009–2010 wet period was variable among wetlands (mean = 1.13 ha, SD = 14.64, CV = 1,289%). The distribution of surface area change was peaked between -1 ha to 1 ha (kurtosis = 11.7; percentiles were 5<sup>th</sup> = -11.67 ha, 25<sup>th</sup> = -1.53 ha, 50<sup>th</sup> = -0.48 ha, 75<sup>th</sup> = 1.06 ha, 95<sup>th</sup> = 20.04 ha). Change in surface area was different among regions ( $F_{2,144} = 3.42$ ,  $P = 0.035$ ; Figure 5) with an overall increase in NGP ( $t = 2.05$ ,  $P = 0.042$ ) but no overall regional change in COT and RRV ( $|t_s| < 1.8$ ,  $P_s > 0.060$ ; Figure 5).

We evaluated the effect of historic wetland drainage on rates of wetland growth (surface area increase) in 122 wetlands. Our final model included the treatment effect of catchment drainage-by-climate phase interaction, catchment drainage-by-basin-full interaction, basin-full-by-climate phase interaction, maximum depth-by-climate phase interaction, and the random error term (Table 3). Our

model had more support (Akaike model weight ( $w_i$ ) = 1,  $K = 11$ ) than a null model ( $\Delta AIC_c = 151$ ,  $w_i = 0$ ,  $K = 3$ ), and the final model explained 50%, 9%, and 49% of the variability of wetland growth rates within the observations overall, within the drying phase, and within the wetting phase, respectively (Table 4). Rate of wetland growth was greater in high drainage catchments than low drainage catchments during both climate phases when the focal wetland initially filled less of the topographic basin (Figure 6). Whereas, the rate of wetland growth was lower in high drainage catchments than low drainage catchments during both climate phases when the focal wetland was initially near the basin spill point (Figure 6). Rates of surface area change diverged at ~2% catchment drainage within wetlands that filled less of their topographic basin (Figure 7).

### **Wetland Depth**

We evaluated changes in water depth in 140 randomly selected wetlands that were sampled in 2004 or 2005 and again in 2010. Change in water depth was variable among wetlands (mean = 0.66 m, SD = 0.76, CV = 115%). The distribution of change was skewed toward increased water levels (skewness = 1.37; percentiles were 5<sup>th</sup> = -0.28 m, 25<sup>th</sup> = 0.16 m, 50<sup>th</sup> = 0.52 m, 75<sup>th</sup> = 0.96 m, 95<sup>th</sup> = 2.30 m). Mean change was not different among regions ( $F_{2, 137} = 0.34$ ,  $P = 0.71$ ; Figure 8) and was greater than zero in all regions (all  $t_s > 2.43$ ,  $P_s < 0.05$ ; Figure 8).

We evaluated changes in water depth between consecutive wet years of 2010 and 2011 within 131 wetlands. Change in depth was variable among wetlands (mean = 0.35 m, SD = 0.43, CV = 123%). The distribution of change was peaked between 0 and 0.6 m change (kurtosis = 5.93; percentiles were 5<sup>th</sup> = -0.05 m, 25<sup>th</sup> = 0.10 m, 50<sup>th</sup> = 0.23 m, 75<sup>th</sup> = 0.49 m, 95<sup>th</sup> = 1.19 m). Mean change was greater in COT than in NGP and RRV ( $F_{2, 128} = 6.05$ ,  $P = 0.003$ ; Figure 9) and was greater than zero in COT and NGP ( $t_s > 5.07$ ,  $P_s < 0.001$ ; Figure 9) but not different than zero in RRV ( $t = 0.51$ ,  $P = 0.613$ ; Figure 9).

We evaluated the effects of landscape and climate factors on change in water depth in 124 wetlands. Our final model included percent basin-full, bank slope ( $\ln$ ), catchment area, change in climate index, catchment area-by-change in climate index interaction, and the random error term (Table 5). Our model had more support ( $w_i = 1$ ,  $K = 8$ ) than a null model ( $\Delta AIC_c = 22.3$ ,  $w_i = 0$ ,  $K = 3$ ), and the final model explained 57% of the variability within the observations overall. Water depth increased through the climate cycle in wetlands that initially filled less of their basin, had steeper bank slopes, and were in larger catchments under conditions with more precipitation rather than smaller catchments under similar conditions (Table 6).

### **Amphipod Density**

We sampled amphipod densities in 131 randomly selected wetlands. *Gammarus* were present in 35%, 26%, and 32% of wetlands in 2004 or 2005, in 2010 and 2011, respectively. *Hyalella* were present in 72%, 67%, and 80% of wetlands in 2004 or 2005, in 2010 and 2011, respectively. Amphipods

(*Gammarus* or *Hyalella*) were present in 77%, 73%, and 84% of wetlands in 2004 or 2005, in 2010 and 2011, respectively. Both *Gammarus* and *Hyalella* densities were skewed right (Figures 10 and 11). There was weak evidence that density of *Gammarus* varied among regions in each 2004 or 2005, 2010, and 2011 ( $F_{2, 128} = 2.77, P = 0.06$ ;  $F_{2, 128} = 2.43, P = 0.09$ ;  $F_{2, 128} = 1.74, P = 0.18$ , respectively; Figure 12), but *Hyalella* densities appeared similar among regions ( $F_{2, 128} = 0.20, P = 0.82$ ;  $F_{2, 128} = 0.19, P = 0.82$ ;  $F_{2, 128} = 1.10, P = 0.34$ , respectively; Figure 13) and for all amphipods ( $F_{2, 128} = 0.44, P = 0.64$ ;  $F_{2, 128} = 0.87, P = 0.42$ ;  $F_{2, 128} = 1.09, P = 0.34$ , respectively; Figure 14).

We evaluated the effect of landscape modification and water-level fluctuation on change in amphipod density of 2004/05 compared with 2010 and 2011 within 126 wetlands. *Hyalella* decreased in density within wetlands that had high amounts of wetland drainage within their catchments (Table 7). *Hyalella* decreased in density from 2004/05 compared with density in 2010 in wetlands that high amount of wetland area exposed during the 2006–2008 dry period and in wetlands that had low amount wetland area flooded in the 2009–2010 wet period (Table 7). *Hyalella* decreased in density from 2004/05 compared with density in 2011 in wetlands that had moderate wetland area exposed during the 2006–2008 dry period (Table 7). *Gammarus* decreased in density from 2004/05 compared with density in 2011 in wetlands that had high percent of catchment area that was drained wetland (Table 8).

### **Fish Occurrence and Relative Abundance**

We sampled fish communities in 131 wetlands that were visited in 2004 and 2005, at which time fish communities were sampled in 90 of these wetlands (Anteau and Afton 2008; Anteau et al. 2011). Fathead minnows, small fish, large fish and any fish group were present in 45%, 38%, 21%, and 60% of wetlands sampled in 2011, respectively. This was an increase of 13%, 9%, 3%, and 12%, respectively, over that observed in 2004 and 2005 (Anteau and Afton 2008; Anteau et al. 2011). Abundance of fathead minnows, small fish, and fish of any group increased in wetlands from 2004 and 2005 to 2011, but we found only weak evidence of an increase in abundance of large fish for the same time period (Figure 17). Fathead minnows were more abundant in wetlands within highly drained catchments that at least moderately filled their topographic basin than they were in wetlands within less drained catchments that filled less of their basin (Table 9). Overall abundance of fish followed this same pattern of higher abundance in highly drained catchments where wetlands filled more of their basin (Table 9).

### **Cattail Abundance**

Our analyses of emergent vegetation included 124 wetlands. We found no strong correlation among fixed-effect variables in analyses ( $|r| \leq 0.30$ ). The proportion of total wetland area that was covered by cattail was variable among wetlands (mean = 0.177, SD = 0.254, CV = 143%). Coverage was moderately different among regions ( $F_{2, 121} = 2.82; P = 0.063$ ), with greater coverage occurring in NGP than that in COT and RRV (Figure 18). Proportion of the wetland covered by cattail was negatively

correlated with increased water depth from 2004/05 to 2011 ( $\hat{\beta} = -0.131$  m, SE = 0.029), but not correlated with percent catchment area that was drained wetland ( $\hat{\beta} = 0.003$ , SE = 0.008). Cattail coverage was negatively correlated with wetland size ( $\hat{\beta} = -0.029$ , SE = 0.014). We found no evidence that neither bulrush coverage nor other emergent species was correlated with either change in depth ( $\hat{\beta} = -0.002$  m, SE = 0.002;  $\hat{\beta} = -0.131$  m, SE = 0.029; respectively) or percent catchment drainage ( $\hat{\beta} = -0.007$ , SE = 0.008;  $\hat{\beta} = -0.131$ , SE = 0.029; respectively). We did not find evidence of wetland size being correlated with coverage by bulrush or other emergent vegetation type ( $\hat{\beta} = 0.000$ , SE = 0.004;  $\hat{\beta} = 0.000$ , SE = 0.001; respectively). Cattail was the dominant emergent vegetation group under all conditions of catchment drainage and water depth change where coverage was greater than zero (Table 10).

## **Discussion**

We found that both catchment drainage and the amount that the focal wetland filled its topographic basin influenced the rate of water surface area change during drying and wetting phases. After controlling for intensity of drying and wetting phases, the disparity between water surface area responses to drying and wetting phase was greatest in wetland with greater amounts of drainage in their catchment and those that were not near their spilling point. Accordingly, it appears that basins that are still hydrologically isolated increase in size through climate cycles (drying and wetting phases) proportional to the amount of drainage in their catchments. However, changes in water surface area offset one another during drying and wetting phases in wetlands that were hydrologically isolated and had minimal amounts of drainage in their catchments. This result suggests that wetlands in modified landscapes are likely to increase in water surface area through consecutive climate cycles, until the water level reaches the elevation of a basin spill point and effectively lose surface-water isolation. Water surface-area dynamics generally decreased in those wetlands that are near their natural or artificial spilling point. Based on these results, it is possible that historic drainage of wetlands within catchments of remaining semipermanent and permanent wetlands likely contributes to a successional change of these wetlands toward a more-permanent lake-phase (Weller and Spatcher 1965). Further, if there has been a shift toward more wetlands in a lake-phase, then productivity of wetlands has likely been reduced due to a lack of water-level fluctuations that drive nutrient cycling (Euliss et al. 1999). This change in wetland hydroperiod could be a major contributing factor toward sustained low densities of amphipod in the region and subsequently can effect waterbird populations within the region.

The climatic wetland hydrology index we used indicated wetter conditions during 2009–2010 than in 2003–2005. While, on average, wetlands were deeper during 2010 and 2011 than they were in 2004 and 2005, the individual increases in depth were less the closer the wetland was to its spilling point.

Wetlands that filled more of their basin likely have reached a stabilized level and any addition of water spills out of the basin, potentially into a lower basin or watershed.

We found cattail coverage was greater in wetlands where water depth changed less. This is consistent with other reports of stabilization of water-levels to be favorable to cattail abundance (Swanson 1992; Galatowitsch et al. 1999; Shay et al. 1999; Boers and Zedler 2008). Because native plant communities in prairie pothole wetlands likely are the result of equilibrium among species that have various degrees of adaptation to dynamic water levels (LaBaugh et al. 1987; Swanson 1992; Euliss et al. 1999), water-level stabilization can lead to long-term changes in the structure of these communities that potentially results in monotypic stands of cattail. Changes in vegetation structure might have a negative impact on use of wetlands by wading birds that require shoreline habitat where they forage within a narrow range of shallow water (Skagen et al. 1999; Anteau 2012). However, we must note that our selection of wetlands was not random in regards to cattail coverage within semipermanent and permanent wetlands. Wetlands were required to have 120 m diameter of open water to initially be sampled in 2004 and 2005. Wetlands that had greater coverage by emergent vegetation were dropped and a new wetland reselected. The implications of this methodology likely have skewed our results to less coverage by emergent vegetation than exists in the population of semipermanent wetlands within the region. Therefore, our summary of emergent vegetation coverage in wetland is applicable to semipermanent and permanent wetlands that have or had large areas of open water.

The overall increase in wetland depth provided more deep-water habitat that was more suitable for fish to survive and allowed fish to colonize into more wetlands through temporal wetland connections created by higher water-levels. Indeed, we did observe fish in more wetlands and in higher abundances than had been observed in the past (Peterka 1989; Anteau and Afton 2008; Anteau et al. 2011). Further, these increases were correlated with greater drainage of wetlands within catchments of focal wetlands and where focal wetlands filled more of their topographic basin. While in the short term some of the increases in fish could be due to being in a wet period of the climate, over the long term it appears that consolidation drainage has increased fish occurrence and abundance.

Historic estimates of amphipod densities are too sparse to allow for rigorous quantitative comparisons with current densities. However, Anteau and Afton (2008) concluded that densities in 2004 and 2005 likely had declined from historical levels based on comparisons with available amphipod data and marked shifts in lesser scaup diets away from amphipods to lesser-preferred foods (Anteau and Afton 2006; Strand et al. 2008; Anteau and Afton 2009a) and concurrent declines in lipid reserves and lipid acquisition of lesser scaup during spring migration (Anteau and Afton 2004, 2009b, 2011). We quantitatively evaluate our estimates in relation to those of Anteau and Afton (2008) in North Dakota, and our estimates are similar to those reported low estimates. Accordingly, our results suggest that the

potential decline in amphipod densities in North Dakota that Anteau and Afton (2008) observed was not driven by the temporal position in the wet–dry cycle when the data were collected.

While overall amphipod densities during spring 2010 and 2011 generally were similar to those low values during springs 2004 and 2005 (Anteau and Afton 2008), there were changes within individual wetlands that provided us some insight into factors that influenced change in amphipod density. We found evidence that high levels of historic wetland drainage within catchments of remaining wetlands negatively impacted densities of both *Hyalella* and *Gammarus*. We found evidence that water-level drawdown had a negative impact on *Hyalella* densities, perhaps this effect is more related to the availability of over-wintering habitat than it is to cycling of nutrients as previously discussed.

We found amphipod densities in 2010–2011 were similar to those in 2004–2005, and represent densities under what we expected to be more ideal hydrologic conditions than those during the 2004–2005 sampling. We expected wetlands with high water-levels following the 2006–2008 dry period to contain greater nutrient concentrations that would benefit wetland productivity. Indeed, we did observe water-level fluctuations during the climate cycle in wetlands with less drainage within their catchment, yet finding little overall change in amphipod density between sampling periods perhaps suggests that amphipod densities are less tied to climate driven water-level fluctuations than previously thought. Although extremes of climate conditions that occur across decades likely do effect amphipod populations by temporarily reducing available suitable habitat, long-term declines in amphipod density across the region are more likely a result of landscape modifications that affect wetland hydrology. Thus availability of suitable habitat for amphipods in lacustrine wetlands is more-permanently reduced. In follow-up analyses to this study we will further seek methods to evaluate the impact of landscape modifications on amphipod abundance and presence of suitable habitat.

Drainage and consolidation of wetlands contributed to an increase surface area of semipermanent and permanent wetlands. Our evidence suggests that wetlands in this modified landscape are likely to continue to increase in size until they reach a spill point and become a larger consolidated wetland system. Further, our results indicate a decrease in amphipod densities in wetlands within these modified catchments. Moreover, we observed an increase in fish abundance with increased water-levels and greater coverage of wetland area by cattail where water-levels stabilized. In a landscape where more wetlands increase to a size in which they become connected to adjacent wetlands and maintain stable water-levels as part of a consolidated wetland system, the number of quality wetlands available to waterbirds is likely to diminish. Semipermanent wetlands historically interacted within a complex of wetlands of various hydroperiods that mostly lacked surface connection, thus these wetlands fluctuated in water-level in response climate variability at different temporal rates. These complexes of interacting wetlands are potentially an integral facet of the region’s ability to support waterbird populations

throughout climate cycles. Where uplands have been modified to create consolidated wetland systems, restoration of wetland complexes of various hydroperiods could prevent further degradation of wetland productivity in the region and could cumulatively improve productivity realized at a regional scale.

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Table 1. Number of wetlands surveyed by Anteau and Afton (2008) in either 2004 or 2005 and by this study in 2010 and 2011; including the total number of wetlands surveyed in 2010 and 2011.

Region	2004/5, 2010 & 2011	2010	2011
Missouri Coteau	44	51	47
Northern Glaciated Plains	79	89	83
Red River Valley	8	10	10
Cottonwood Lake Study Area	-	3	3
Total	131	153	143

Table 2. Descriptions of land-cover classes for use in analyses of land use surrounding wetlands.

Land-cover class	Class description
Native grassland	These grasslands have never been broken by a plow. Cattle grazing may occur on these lands. The presence of many scattered rocks, when visible, is a good indicator.
Restored grassland	These lands have been returned to grass after having been cultivated. Often these lands are in conservation/restoration programs (native and non-native plantings). The presence of rock piles within or immediately adjacent is a good indicator. Lands that have been improved for pastures or other grassland uses are included.
Unknown grassland	These are grasslands that cannot be identified as native versus restored.
Hayland	These lands are dedicated to production of hay, primarily alfalfa or other monotypic forms. These do not include native or restored grasslands that have been mowed. These lands are hayed once or more annually.
Cropland	These lands are currently cultivated for production of crops (e.g., row crops, small grains). Fallow fields are included. Agriculture on these lands may include annual conventional till, non-conventional till, or no-till practices.
Shrubs	These lands have overhead coverage dominated by woody shrubs <3 m in height.
Trees	These lands have overhead coverage dominated by trees >3 m in height.
Developed	These lands have been developed into urban areas, commercial developments, residential developments, or farmsteads. These include monotypic grass lawns. Livestock feed lots are included. Maintained roads (two-track, prairie trails are not detected).
Barren	These lands have barren soil as a result of mining or similar practices.
Wetland	Open water and vegetated, saturated soil areas including rivers, streams, lakes, ponds, and marshes.

Table 3. Reduction of covariates from our *a priori* model used to examine the effect of catchment drainage on surface area dynamics in wetlands of North Dakota during a drying and a wetting phase of a climate cycle. Changes in model log likelihood ( $\Delta LL$ ), number of estimated parameters ( $\Delta K$ ), and Akaike's Information Criterion for small sample size ( $\Delta AIC_c$ ) are reported for the model with that variable removed relative to the referenced full model. We deemed covariates important (IMP) if their removal causes a  $>2 \Delta K$  increase in  $AIC_c$ . A colon indicates an interaction between variables.

Covariate Removed	$\Delta LL$	$\Delta K$	$\Delta AIC_c$	IMP
Catchment Drainage : Basin-Full	-13.4	1	24.4	Yes
Basin-Full : Phase	-7.6	1	12.9	Yes
Basin-Full	-32.9	3	58.8	Yes
Max. Depth : Phase	-4.6	1	6.8	Yes
Max. Depth	-5.8	2	6.9	Yes
Cropland : Phase	-1.2	1	0.1	No
Cropland	-1.6	2	-1.5	No
Bank Slope : Phase	-1.2	1	0.1	No
Bank Slope	-1.2	2	-2.2	No
Climate : Phase	-0.4	1	-1.5	No
Climate	-0.5	2	-3.7	No
Catchment Area : Phase	-0.7	1	-1.0	No
Catchment Area	-0.7	2	-3.3	No

<sup>a</sup> Full model  $LL = -120.3$ ,  $K = 19$ ,  $AIC_c = 282.0$

Table 4. Estimated coefficients ( $\hat{\beta}$ ), standard errors (SE), lower 85 % confidence limit (LCL), and upper 85 % confidence limit (UCL) for fixed effects within the final model used to examine the effect of catchment drainage on water surface area dynamics in wetlands of North Dakota during a drying and a wetting phase of a climate cycle.

Fixed Effects	$\hat{\beta}$	SE	LCL	UCL
Intercept	-0.2502	0.1891	-0.5225	0.0220
Catchment Drainage	-0.2330	0.0433	-0.2953	-0.1707
Wetting Phase	0.3708	0.2579	-0.0005	0.7420
Basin-Full	0.1760	0.0556	0.0959	0.2561
Maximum Depth	0.2051	0.0527	0.1293	0.2809
Catchment Drainage : Wetting Phase	-0.0137	0.0209	-0.0437	0.0164
Basin-Full : Wetting Phase	-0.2711	0.0653	-0.3652	-0.1771
Catchment Drainage : Basin-Full	-0.0890	0.0164	-0.1126	-0.0654
Maximum Depth : Wetting Phase	-0.2866	0.0745	-0.3938	-0.1793

Table 5. Reduction of variables from our *a priori* model used to examine the effect of landscape and climate factors on water depth change in wetlands of North Dakota through a recent climate cycle. Changes in model log likelihood ( $\Delta LL$ ), number of estimated parameters ( $\Delta K$ ), and Akaike's Information Criterion for small sample size ( $\Delta AIC_c$ ) are reported for the model with that variable removed relative to the referenced full model. We deemed covariates important (IMP) if their removal causes a  $>2 \Delta K$  increase in  $AIC_c$ . A colon indicates an interaction between variables.

Variable	$\Delta LL$	$\Delta K$	$\Delta AIC_c$	IMP
Climate Index	-6.3	2	7.7	Yes
Bank Slope	-4.0	1	5.6	Yes
Basin-Full	-4.9	2	4.9	Yes
Catchment Area	-4.7	2	4.5	Yes
Catchment Area : Climate Index	-2.8	1	3.1	Yes
Cropland	-0.1	1	-2.3	No
Catchment Drainage : Basin-Full	0.0	1	-2.4	No
Surface Connections	0.0	1	-2.4	No
Catchment Drainage	-0.1	2	-4.8	No

<sup>a</sup> Full model LL = -117.7, K = 12,  $AIC_c$  = 262.1



Table 6. Estimated coefficients ( $\hat{\beta}$ ), standard errors (SE), lower 85 % confidence limit (LCL), and upper 85 % confidence limit (UCL) for fixed effect variables within the final model used to examine the effect of landscape and climate factors on water depth change in wetlands of North Dakota through a recent climate cycle.

Variable	$\hat{\beta}$	SE	LCL	UCL
Intercept	2.0544	0.4076	1.4676	2.6412
Basin-Full	-0.0070	0.0021	-0.0101	-0.0040
Bank Slope	0.1260	0.0412	0.0668	0.1853
Catchment Area	-0.0539	0.0566	-0.1354	0.0276
Climate Index	-0.6624	0.4471	-1.3060	-0.0187
Catchment Area : Climate Index	0.1836	0.0736	0.0776	0.2896

Table 7. Estimated mean effect on change in *Hyalella azteca* density by wetland drainage within the catchment of the focal wetland, wetland area exposed during water drawdown during drying phase and wetland area flooded during wetting phase of a recent climate cycle that occurred from 2003–2011. Means estimates were made for change in density from 2004/05 to 2010 and from 2004/05 to 2011. Low, moderate, and high levels of each factor were defined using one-third breaks within the sampled distribution, respectively.

	Low	Moderate	High
<b>Catchment Drainage</b>			
2010	-1.25 ( -5.14, 0.21)	-0.31 ( -2.59, 1.09)	-3.36 (-10.83, -0.61)
2011	-0.65 ( -3.79, 0.75)	-0.04 ( -1.99, 1.79)	-2.81 ( -9.92, -0.33)
<b>Drawdown</b>			
2010	0.22 ( -1.45, 2.65)	-1.06 ( -4.78, 0.37)	-6.41 (-21.82, -1.41)
2011	0.82 ( -0.97, 5.52)	-3.01 (-11.28, -0.31)	-1.98 ( -9.84, 0.22)
<b>Flooding</b>			
2010	-5.17 (-17.45, -1.06)	-0.35 ( -2.82, 1.09)	-0.54 ( -3.76, 1.01)
2011	-1.65 ( -8.87, 0.40)	-0.27 ( -2.89, 1.40)	-0.91 ( -5.81, 0.86)

Table 8. Estimated mean effect on change in *Gammarus lacustris* density by wetland drainage within the catchment of the focal wetland, wetland area exposed during water drawdown during drying phase and wetland area flooded during wetting phase of a recent climate cycle that occurred from 2003–2011. Means estimates were made for change in density from 2004/05 to 2010 and from 2004/05 to 2011. Low, moderate, and high levels of each factor were defined using one-third breaks within the sampled distribution, respectively.

		Low	Moderate	High
<b>Catchment Drainage</b>				
	2010	0.00 (-0.65, 0.66)	-0.16 (-0.93, 0.42)	-0.74 (-1.86, -0.05)
	2011	0.09 (-0.63, 0.93)	-0.18 (-1.09, 0.50)	-0.34 (-1.37, 0.31)
<b>Drawdown</b>				
	2010	-0.23 (-1.12, 0.41)	0.04 (-0.61, 0.74)	-0.69 (-1.96, 0.04)
	2011	0.07 (-0.86, 1.12)	-0.09 (-0.99, 0.68)	-0.42 (-1.85, 0.41)
<b>Flooding</b>				
	2010	-0.67 (-1.89, 0.03)	0.27 (-0.33, 1.13)	-0.50 (-1.64, 0.17)
	2011	-0.38 (-1.81, 0.47)	0.47 (-0.25, 1.68)	-0.52 (-2.00, 0.31)

Table 9. Back-transformed geometric mean catch per unit effort of fathead minnows and any fish species (95% CI) captured in semipermanent and permanent prairie pothole wetlands in North Dakota during springs of 2004, 2005 and 2011. Means were estimated for combinations of low, moderate, and high levels of both catchment drainage and percent basin filled by focal wetland.

Catchment Drainage	Basin Full	Fathead Minnow	Any Fish
Low	Low	0.302 (-0.008, 0.708)	0.617 (0.194, 1.188)
	Moderate	0.567 ( 0.243, 0.975)	0.912 (0.480, 1.471)
	High	0.826 ( 0.356, 1.459)	1.196 (0.574, 2.064)
Moderate	Low	0.371 ( 0.061, 0.773)	0.754 (0.318, 1.335)
	Moderate	0.651 ( 0.354, 1.014)	1.075 (0.667, 1.582)
	High	0.924 ( 0.479, 1.504)	1.383 (0.777, 2.197)
High	Low	0.615 ( 0.142, 1.285)	1.265 (0.538, 2.335)
	Moderate	0.944 ( 0.481, 1.553)	1.679 (0.981, 2.624)
	High	1.266 ( 0.685, 2.047)	2.077 (1.210, 3.283)

Table 10. Estimated mean coverage of wetland area by emergent vegetation types (proportion; 95% CI) in semipermanent and permanent wetlands within the Prairie Pothole Region of North Dakota in 2011. Means were estimated for combinations of low, moderate, and high levels of drainage within the catchment and change in water depth between 2004 or 2005 and 2011.

Catchment Drainage	Water Depth Change	Cattail	Bulrush	Other Species
Low	Low	0.260 ( 0.192, 0.329)	0.025 ( 0.008, 0.043)	0.009 ( 0.002, 0.016)
	Moderate	0.184 ( 0.130, 0.239)	0.021 ( 0.007, 0.035)	0.007 ( 0.001, 0.013)
	High	0.064 (-0.006, 0.134)	0.015 (-0.003, 0.033)	0.004 (-0.004, 0.011)
Moderate	Low	0.266 ( 0.204, 0.328)	0.022 ( 0.007, 0.038)	0.008 ( 0.002, 0.014)
	Moderate	0.190 ( 0.144, 0.236)	0.018 ( 0.007, 0.030)	0.006 ( 0.001, 0.011)
	High	0.069 ( 0.005, 0.134)	0.012 (-0.004, 0.029)	0.002 (-0.004, 0.009)
High	Low	0.284 ( 0.210, 0.359)	0.013 (-0.006, 0.032)	0.004 (-0.004, 0.011)
	Moderate	0.208 ( 0.145, 0.272)	0.009 (-0.007, 0.025)	0.001 (-0.005, 0.008)
	High	0.088 ( 0.007, 0.168)	0.003 (-0.018, 0.023)	-0.002 (-0.010, 0.006)

Figure 1. Palmer Hydrological Drought Index (PHDI; NCDC 2014) for Prairie Pothole Regions of North Dakota from 1 January 1980 through 31 December 2011. These data show periodic moderate to severe drought in 2006–2008 for all climate divisions. The PHDI assess long-term moisture supply.

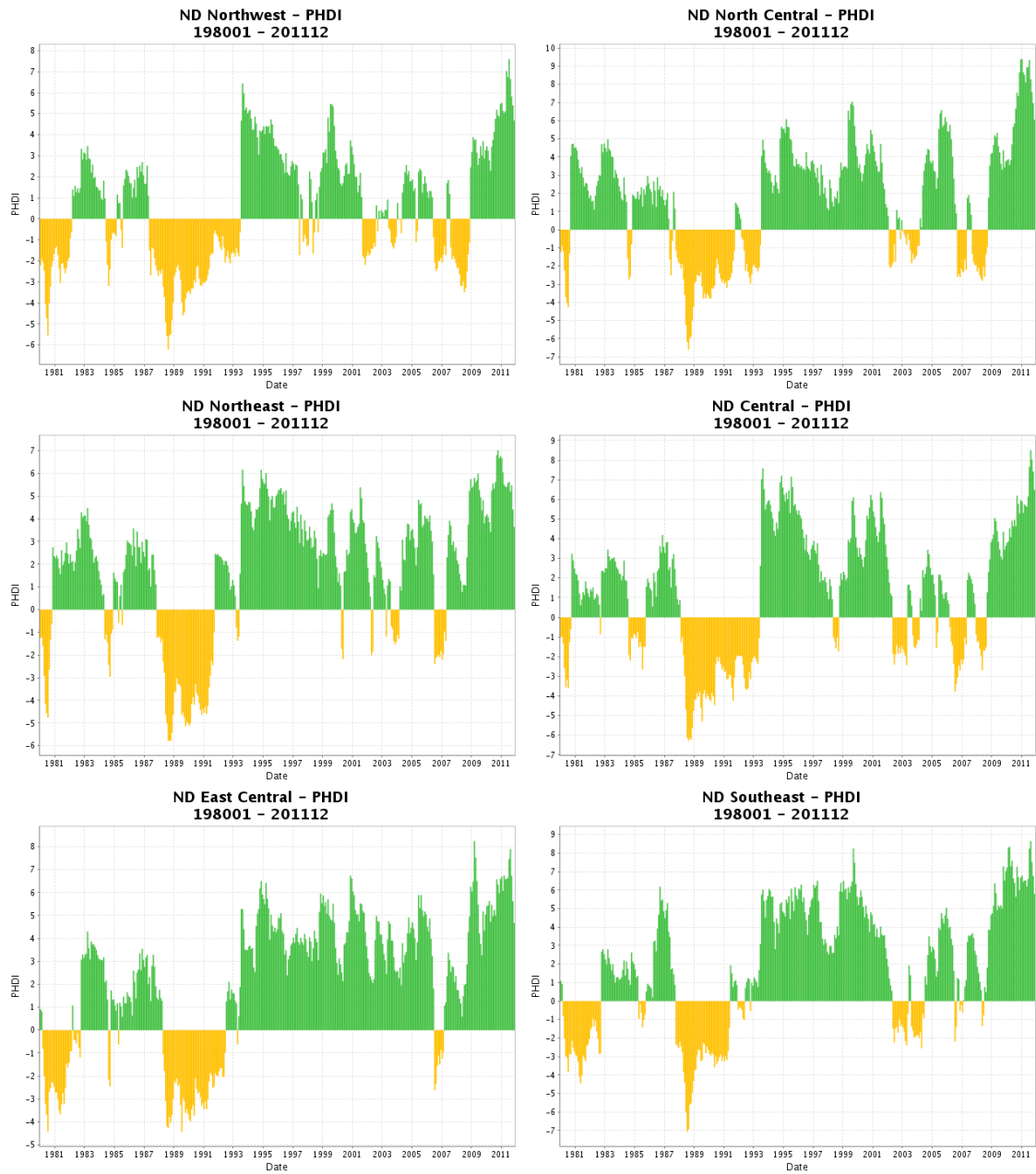


Figure 2. North Dakota study area showing three eco-physiographic regions and townships where wetland sampling will occur during early spring of 2010 and 2011. Townships outlined in blue contain wetlands sampled by Anteau and Afton (2008) in 2004 and 2005 and that will be sampled again during the current study in 2010 and 2011, red are townships selected for supplemental sampling in 2010 and 2011, and green are townships containing the three wetlands sampled at Cottonwood Lake Study Area.

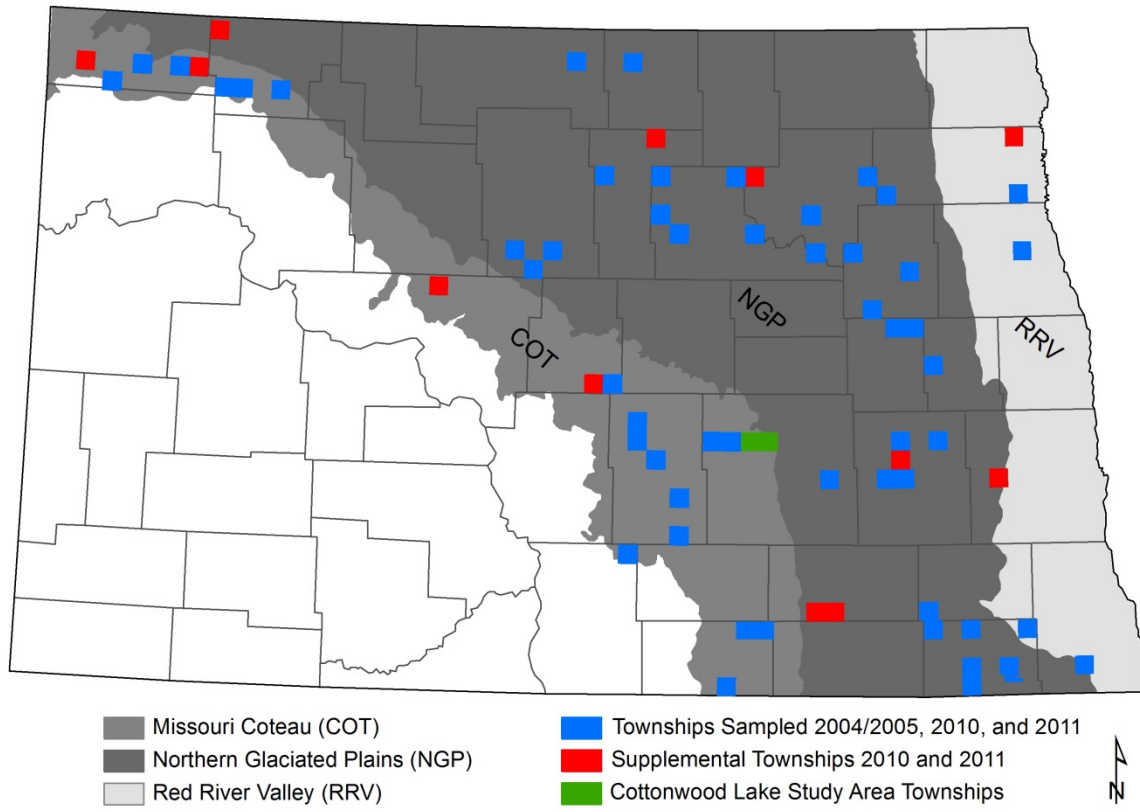


Figure 3. Generalized wetland sampling design (not to scale), including randomly located sampling transects (white solid lines; primary 1–4, secondary 5–10), sweep-net stations (blue dots located 10 and 60 m from emergent vegetation [gray area]), perpendicular sub-transects (black boxed-line; direction is random), water-depth measure stations (red dots), water-quality stations (green dots), and minnow-trap locations (X).

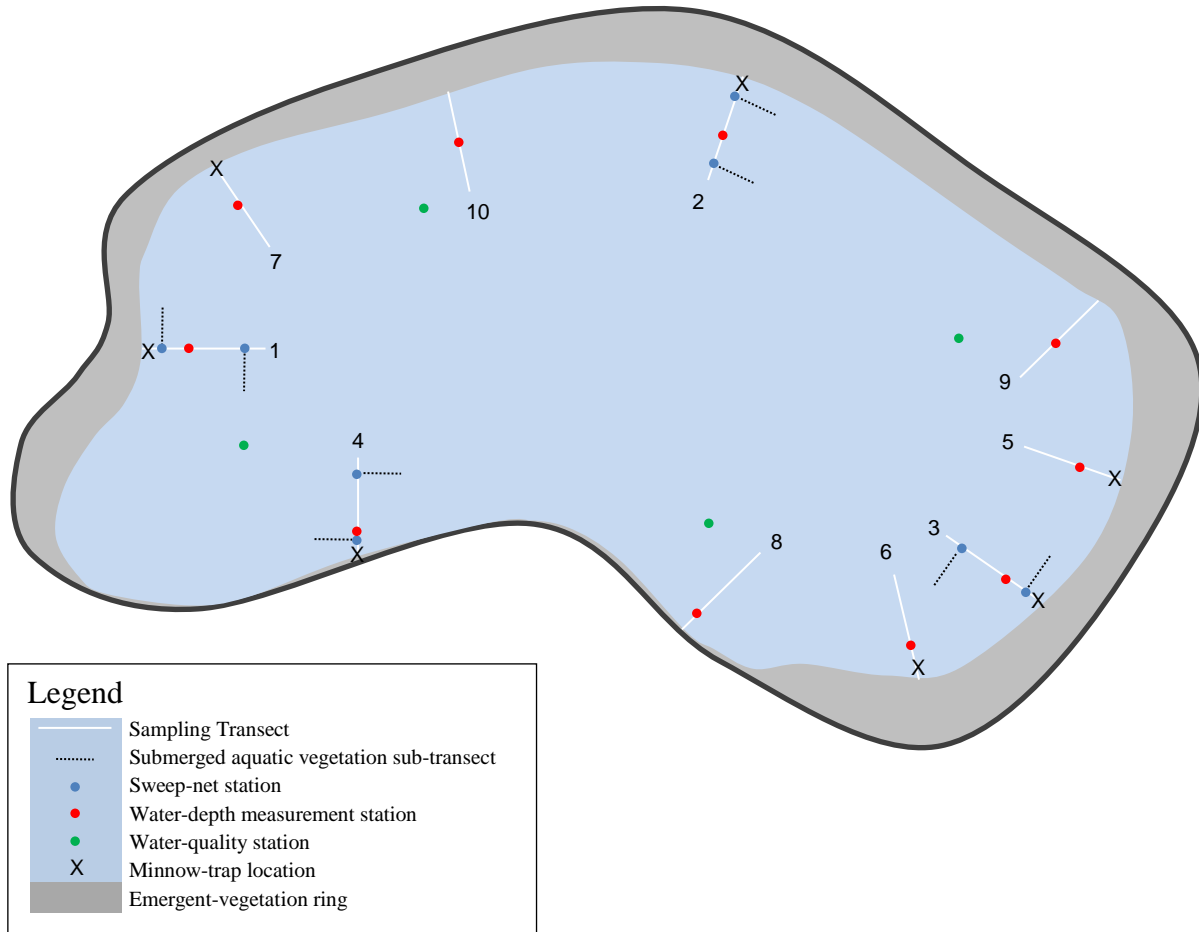




Figure 4. Mean climatic wetland hydrologic index values and 95% confidence intervals for each climate period of the study from the locations of 147 semipermanent and permanent prairie pothole wetlands of North Dakota. We consider a value above zero to be a wet period and a value below zero to be a dry period.



Figure 5. Least-squares mean change in wetland surface area ( $\pm$  95% CI) in 147 wetlands between the wet period of 2003–2005 and the wet period of 2009–2010. Regions are depicted as COT = Missouri Coteau, NGP = Northern Glaciated Plains, and RRV = Red River Valley.

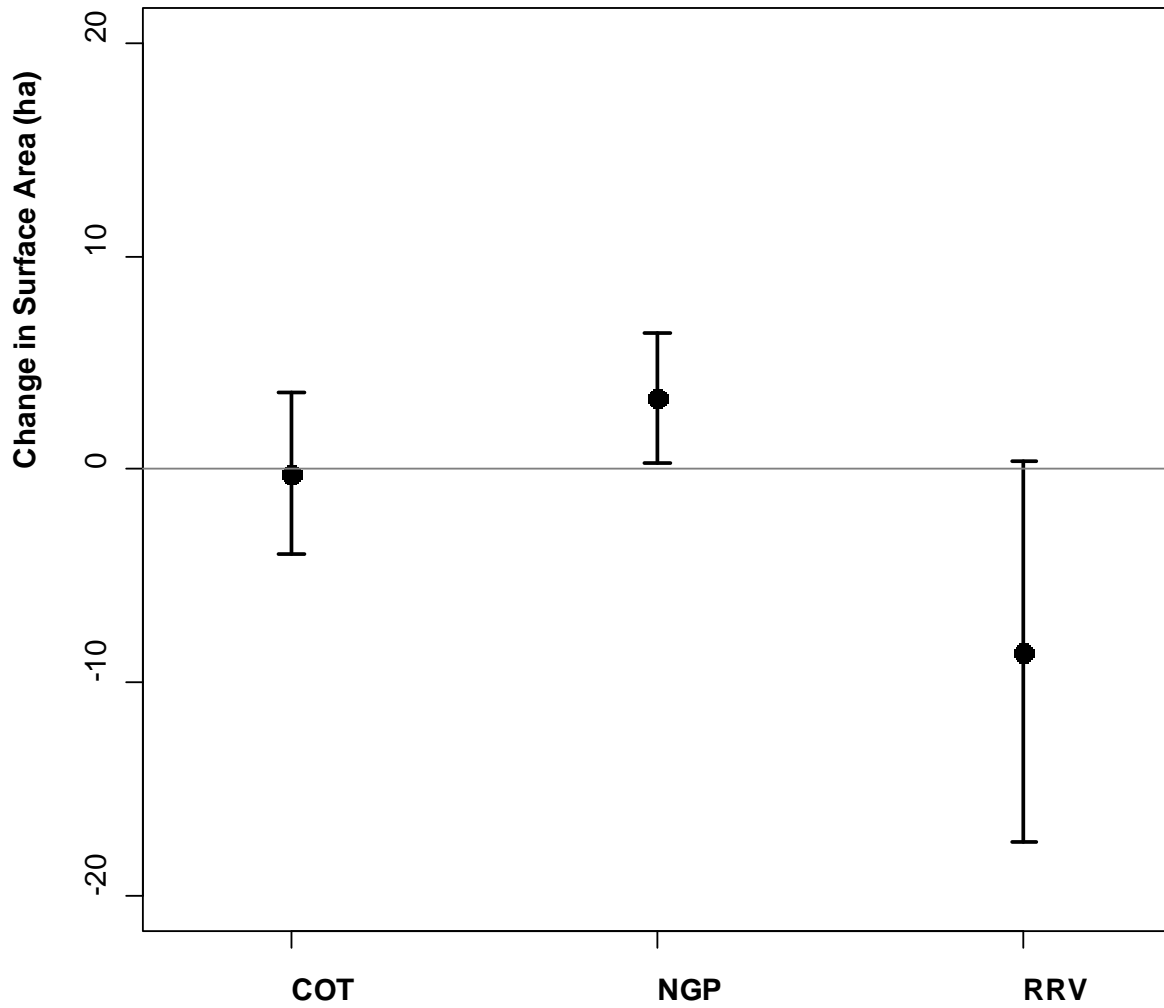


Figure 6. Predicted rate of wetland growth (85% CI) during both the drying and wetting phase for 122 semipermanent and permanent prairie pothole wetlands of North Dakota through a recent climate cycle (2004–2011). Predictions were made for focal wetlands that filled (a) less, (b) moderate, and (c) more of their basin at the start of the climate phase; for the drying phase 51%, 67%, and 90%, and for wetting phase 34%, 50%, 73%, respectively. Model estimates for the drying phase are in gray and for the wetting phase in black. Solid lines represent estimates with a slope different than zero and dashed lines represent estimates with a slope not different than zero.

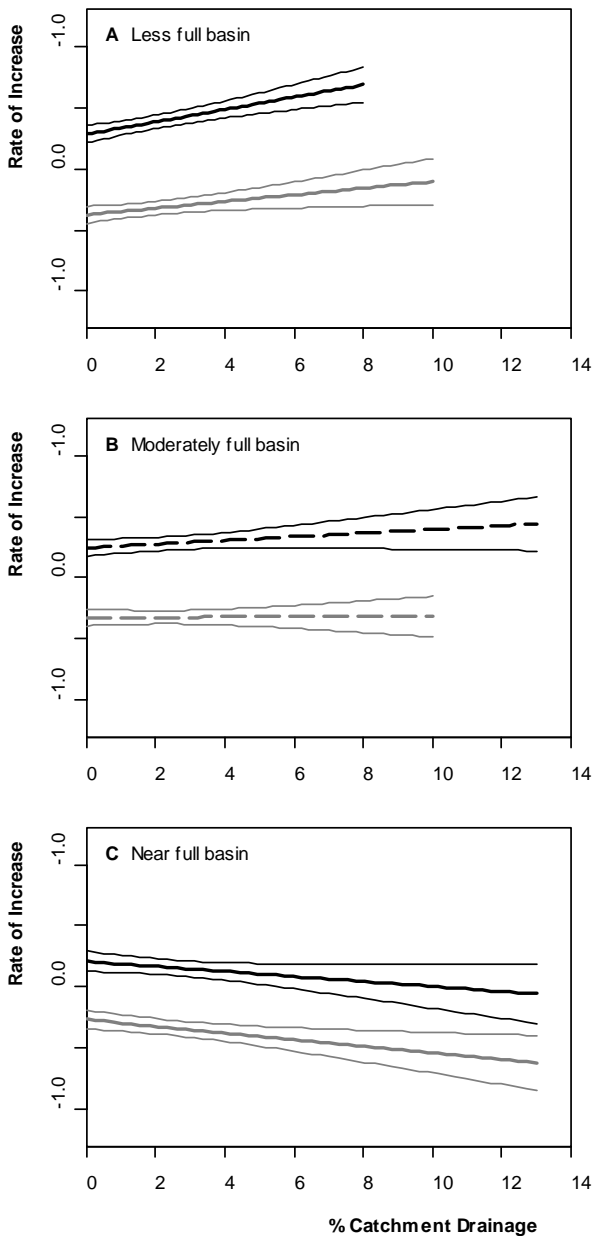


Figure 7. Predicted rate of wetland surface area change during both the drying and wetting phase for 122 semipermanent and permanent prairie pothole wetlands of North Dakota through a recent climate cycle (2004–2011). The drying phase is represented by the lighter gray color and wetting phase by the darker gray color. Rates were predicted for the drying phase over a range of 3–90% of basin filled, because this range represents wetland dynamics less likely to be influenced by artificial drainage pathways in the upper portion of the basin. Predictions for the wetting phase were made over a range of 1–34% of basin filled, because these wetlands remained below the spill point throughout the wetting phase. Wetland water budgets are interpreted to be unbalanced where rate of change estimates do not overlap.

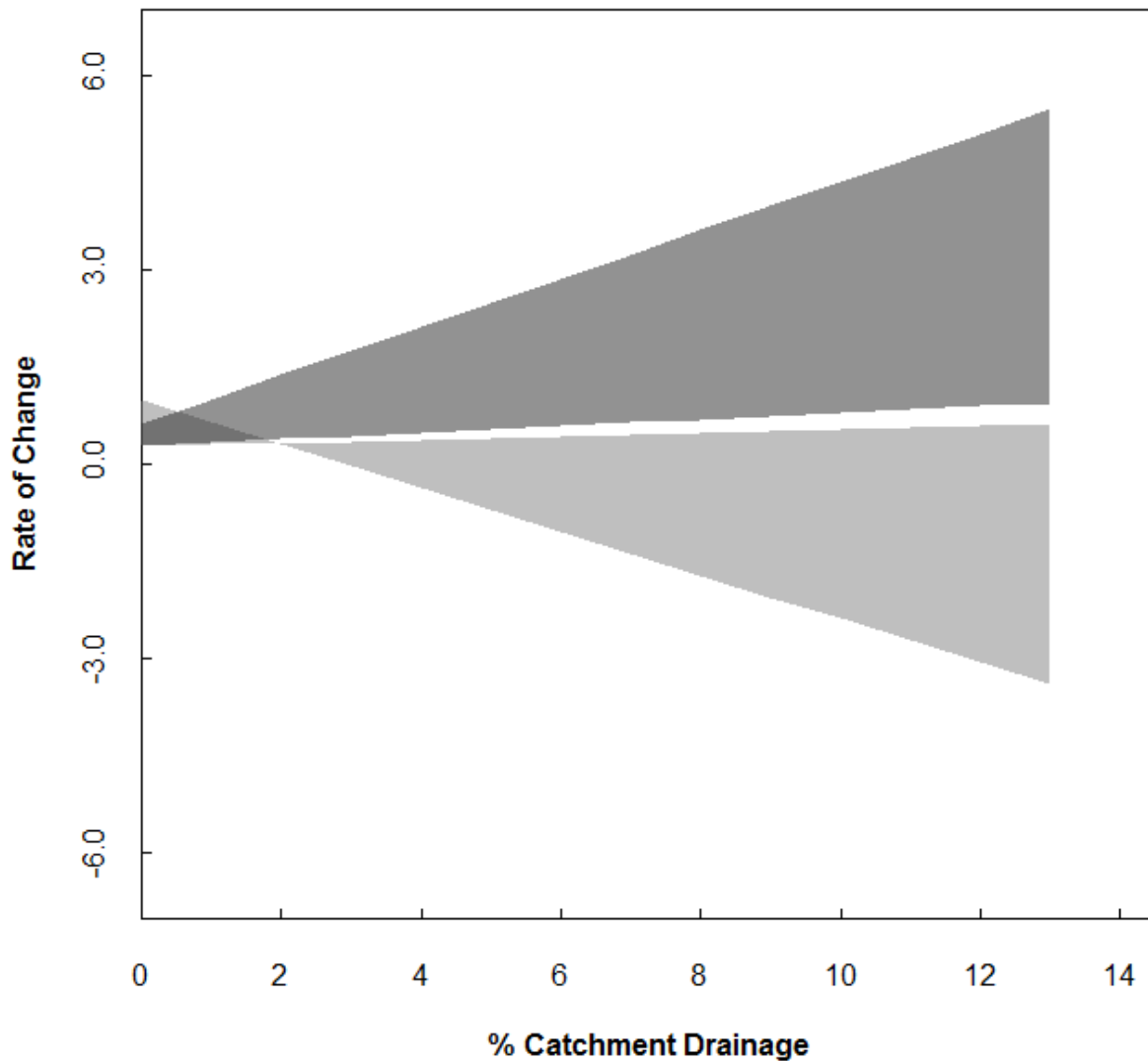


Figure 8. Least-squares mean change in water depth ( $\pm$  95% CI) in 140 randomly selected wetlands between springs of 2004 or 2005 and 2010. Regions are depicted as COT = Missouri Coteau, NGP = Northern Glaciated Plains, and RRV = Red River Valley.

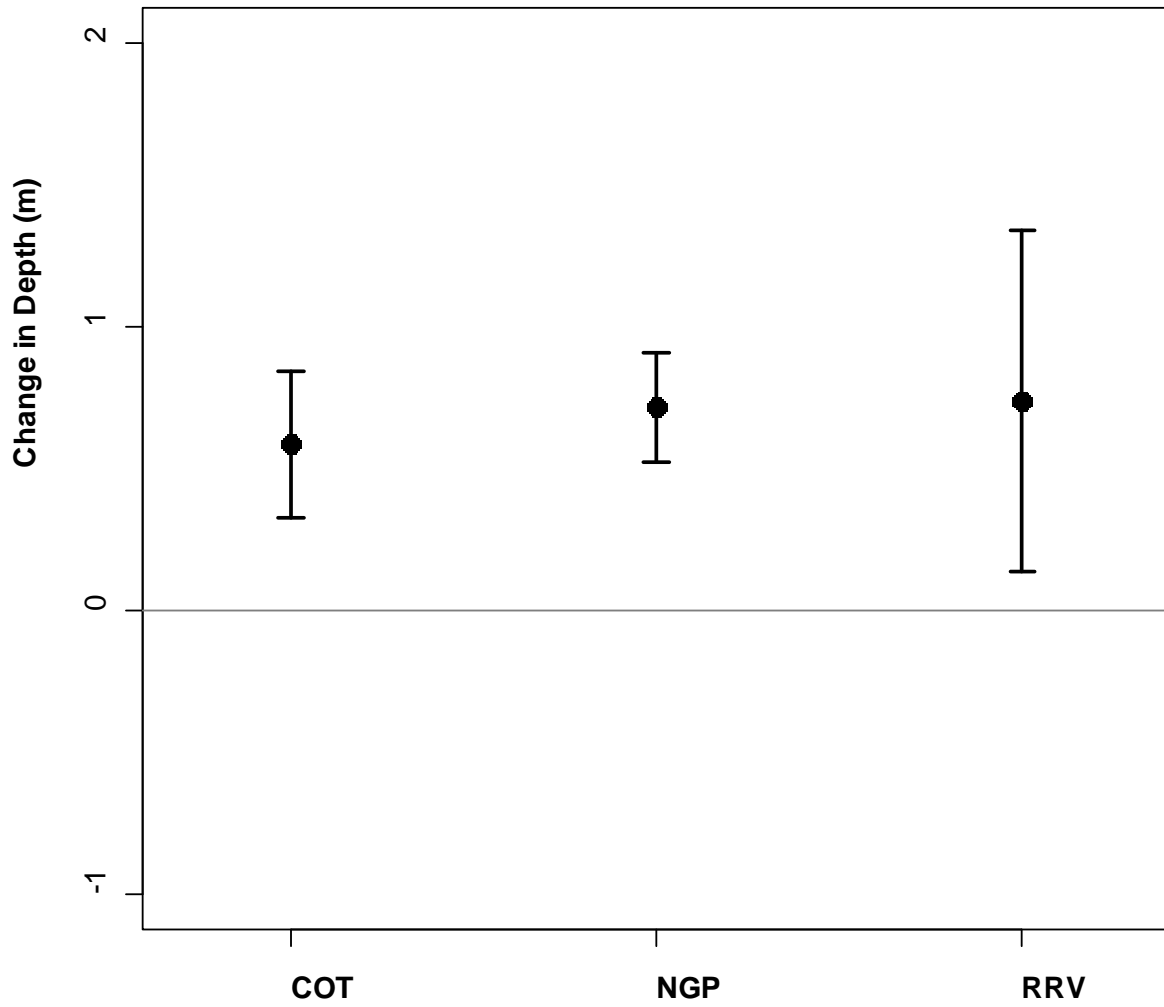


Figure 9. Least-squares mean change in water depth ( $\pm$  95% CI) in 131 randomly selected wetlands between springs of 2010 and 2011. Regions are depicted as COT = Missouri Coteau, NGP = Northern Glaciated Plains, and RRV = Red River Valley.

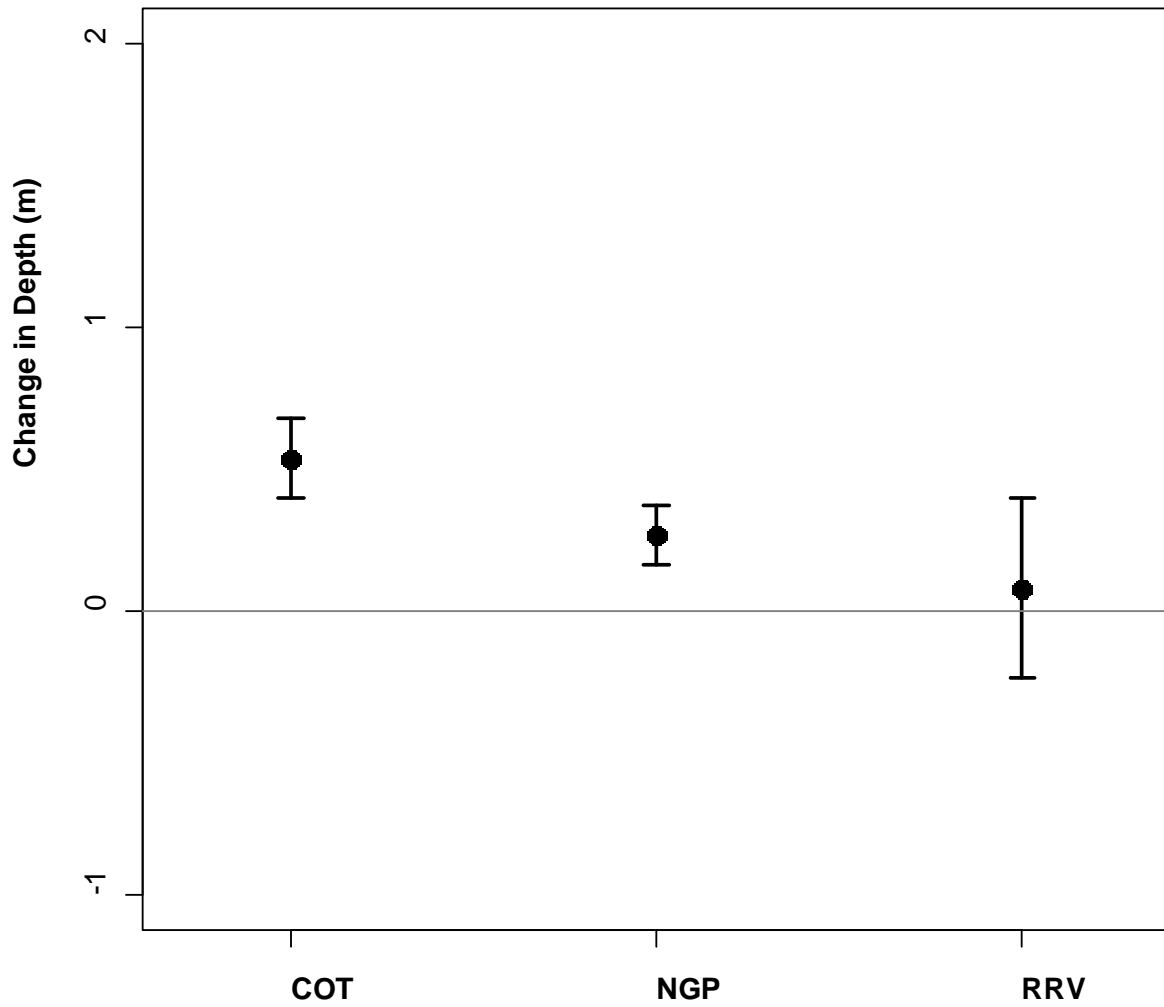


Figure 10: Distribution histogram of *Gammarus lacustris* densities from wetlands sampled within 131 semipermanent and permanent prairie pothole wetlands of North Dakota in 2010 and 2011.

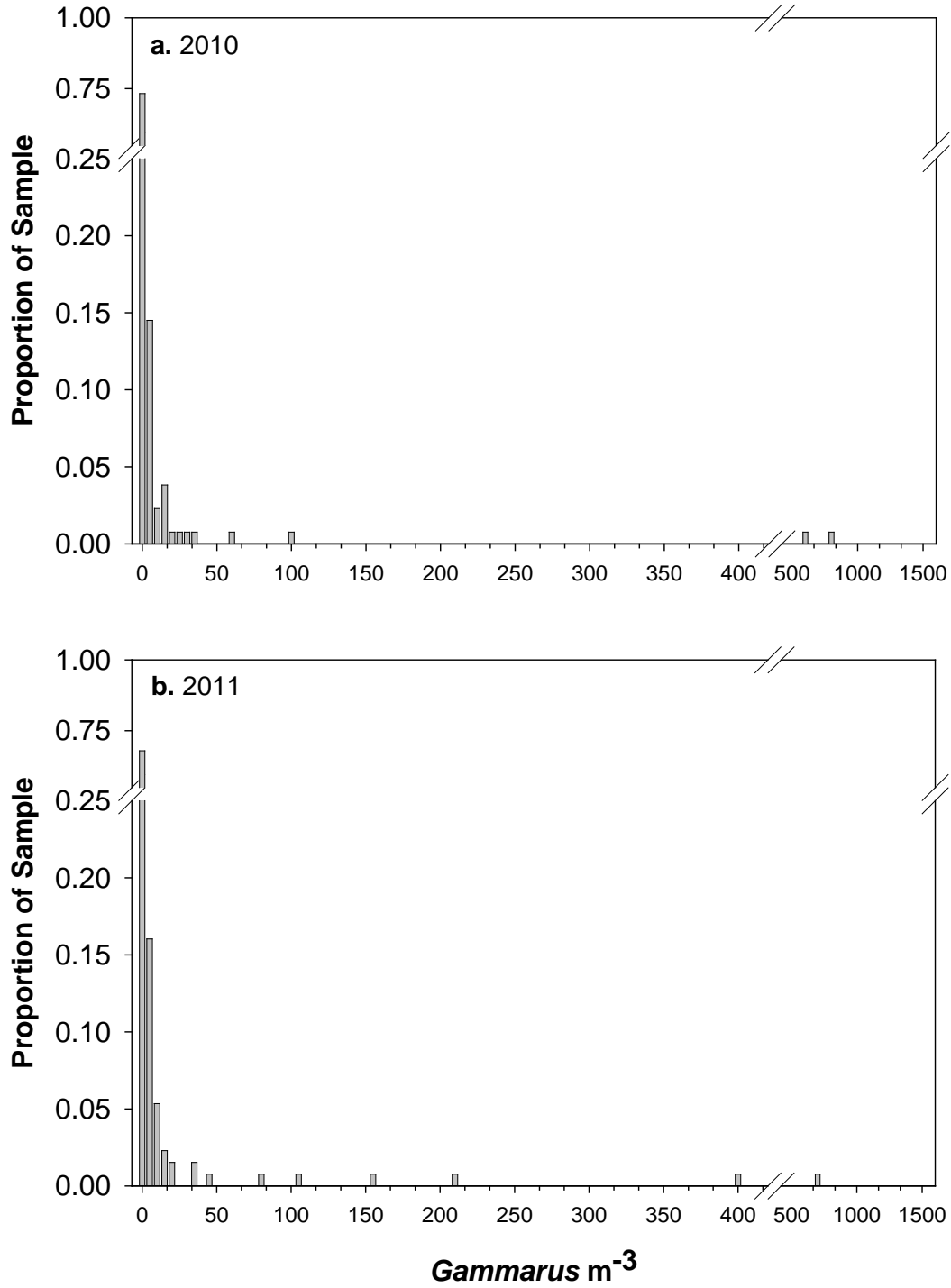


Figure 11: Distribution histogram of *Hyalella azteca* densities from wetlands sampled within 131 semipermanent and permanent prairie pothole wetlands of North Dakota in 2010 and 2011.

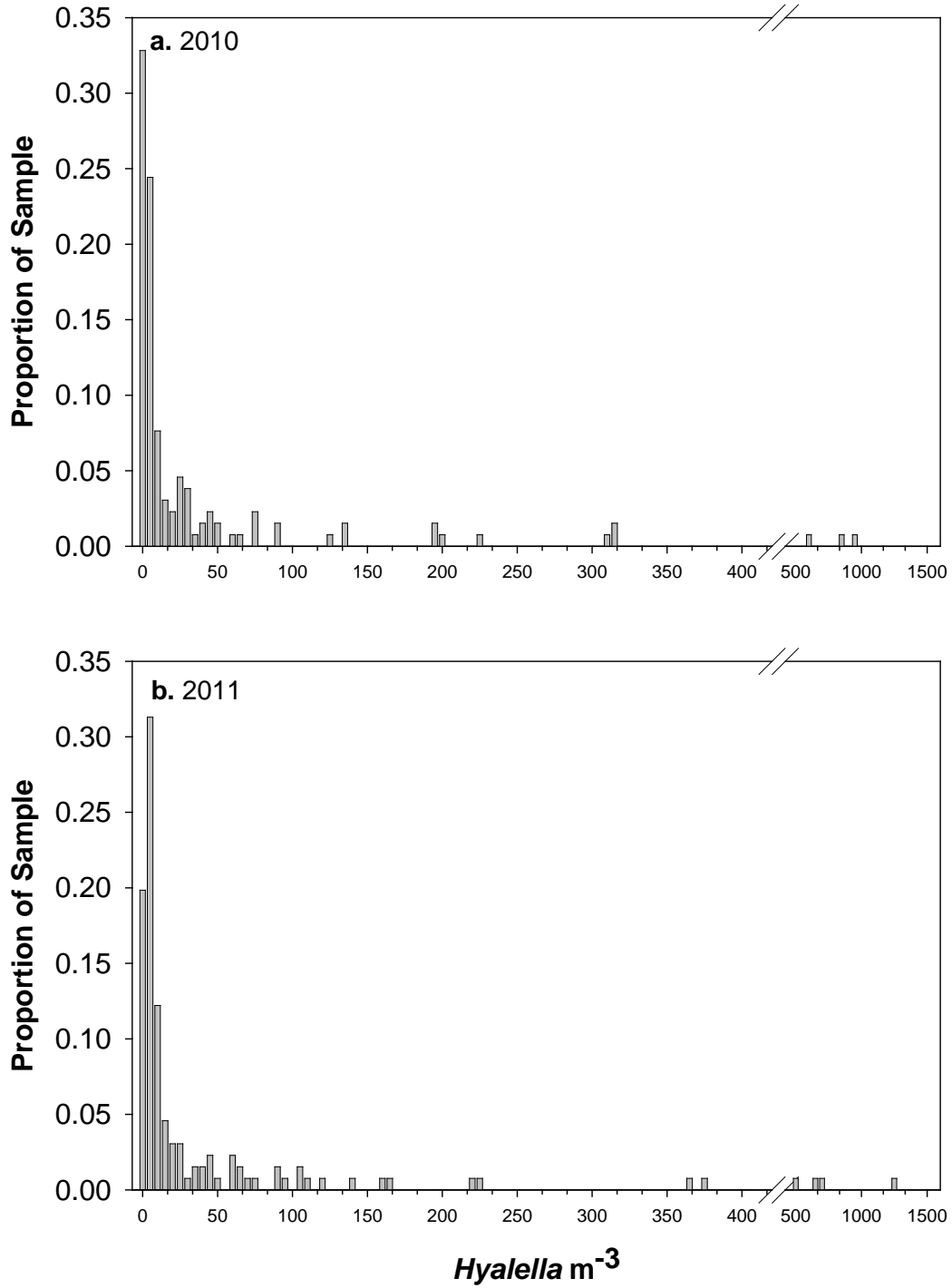




Figure 12. Back-transformed geometric least-squares mean densities ( $\pm$  95% CI) of *Gammarus* in springs of 2004 or 2005 (circle), 2010 (square) and 2011 (triangle) by region of North Dakota (adapted from Anteau and Afton 2008). Regions are depicted as COT = Missouri Coteau, NGP = Northern Glaciated Plains, and RRV = Red River Valley.

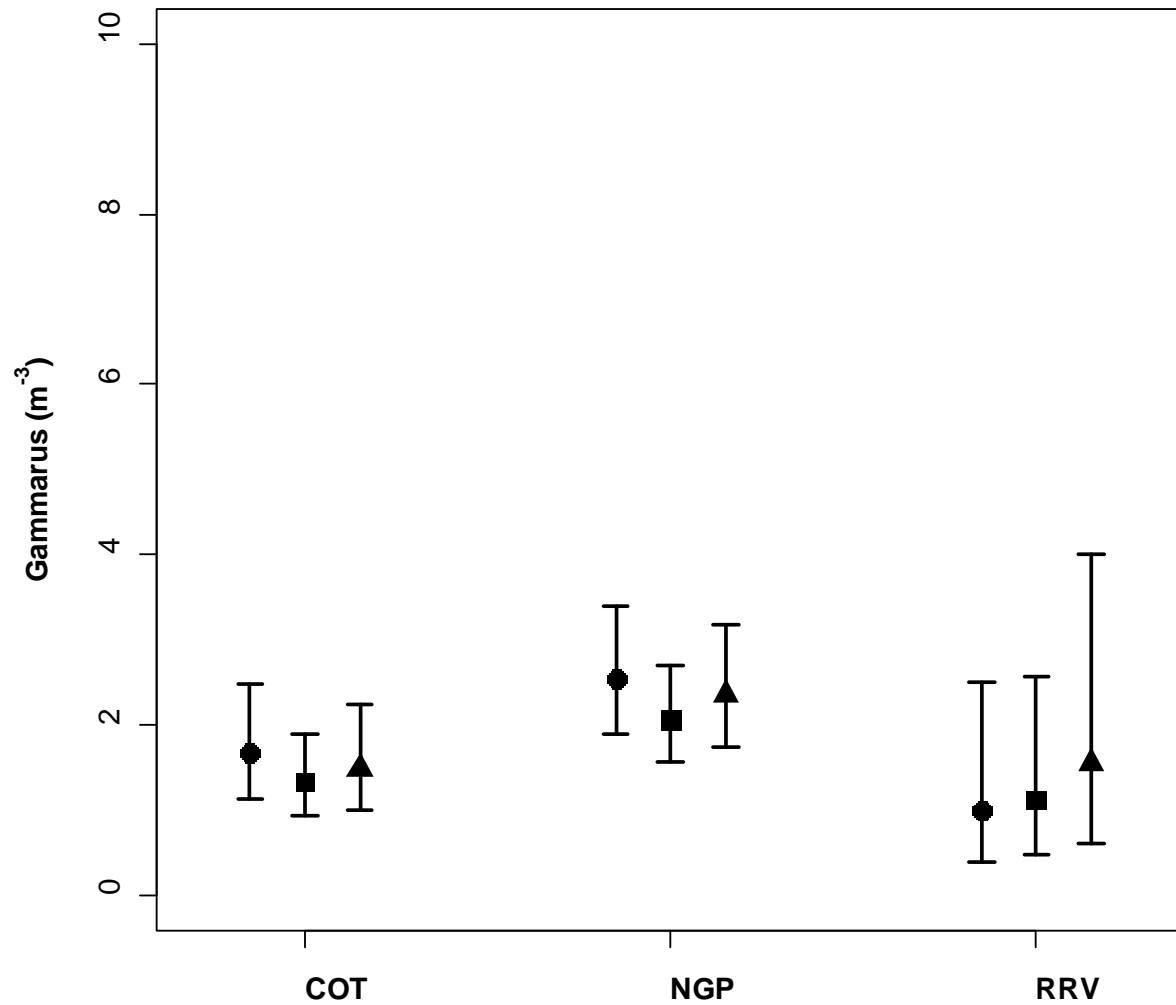


Figure 13. Back-transformed geometric least-squares mean densities ( $\pm$  95% CI) of *Hyalella* in springs of 2004 or 2005 (circle), 2010 (square) and 2011 (triangle) by region of North Dakota (adapted from Anteau and Afton 2008). Regions are depicted as COT = Missouri Coteau, NGP = Northern Glaciated Plains, and RRV = Red River Valley.

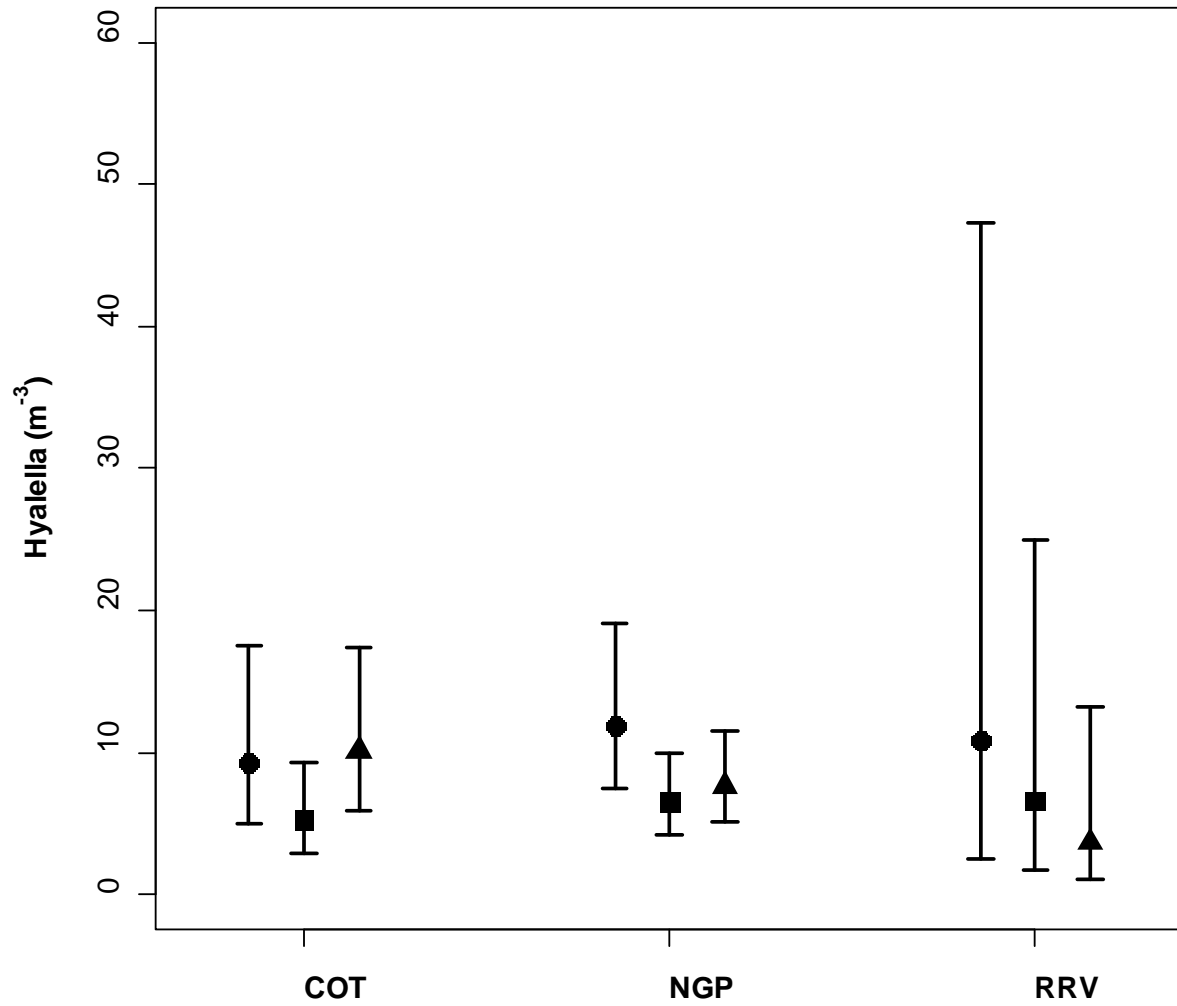


Figure 14. Back-transformed geometric least-squares mean densities ( $\pm$  95% CI) of amphipods (*Gammarus* and *Hyalella* combined) in springs of 2004 or 2005 (circle), 2010 (square) and 2011 (triangle) by region of North Dakota. Regions are depicted as COT = Missouri Coteau, NGP = Northern Glaciated Plains, and RRV = Red River Valley.

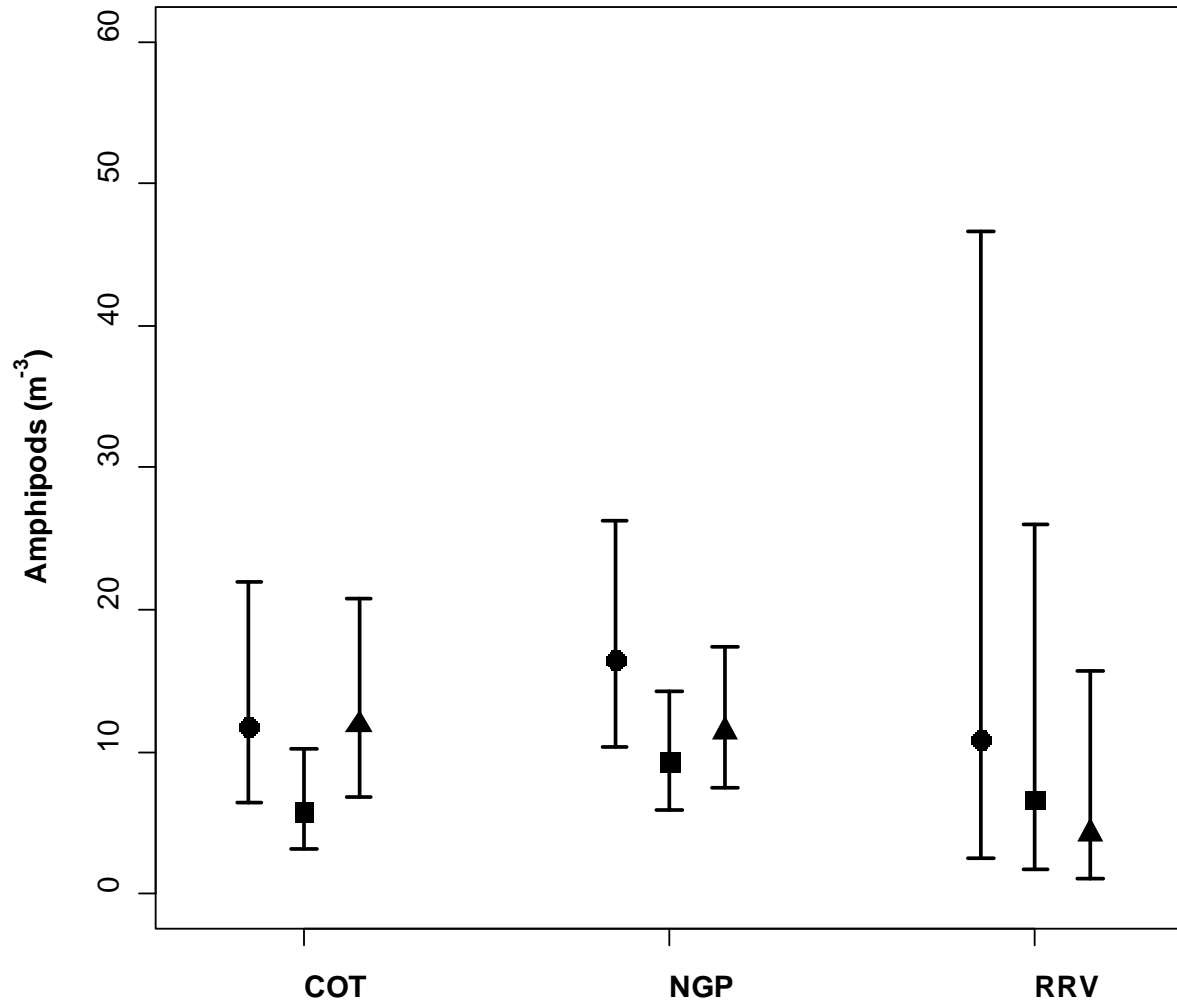


Figure 15. Distribution histogram of change in measured density of *Hyalella azteca* within 124 semipermanent and permanent prairie pothole wetlands of North Dakota from 2004 or 2005 to 2010.

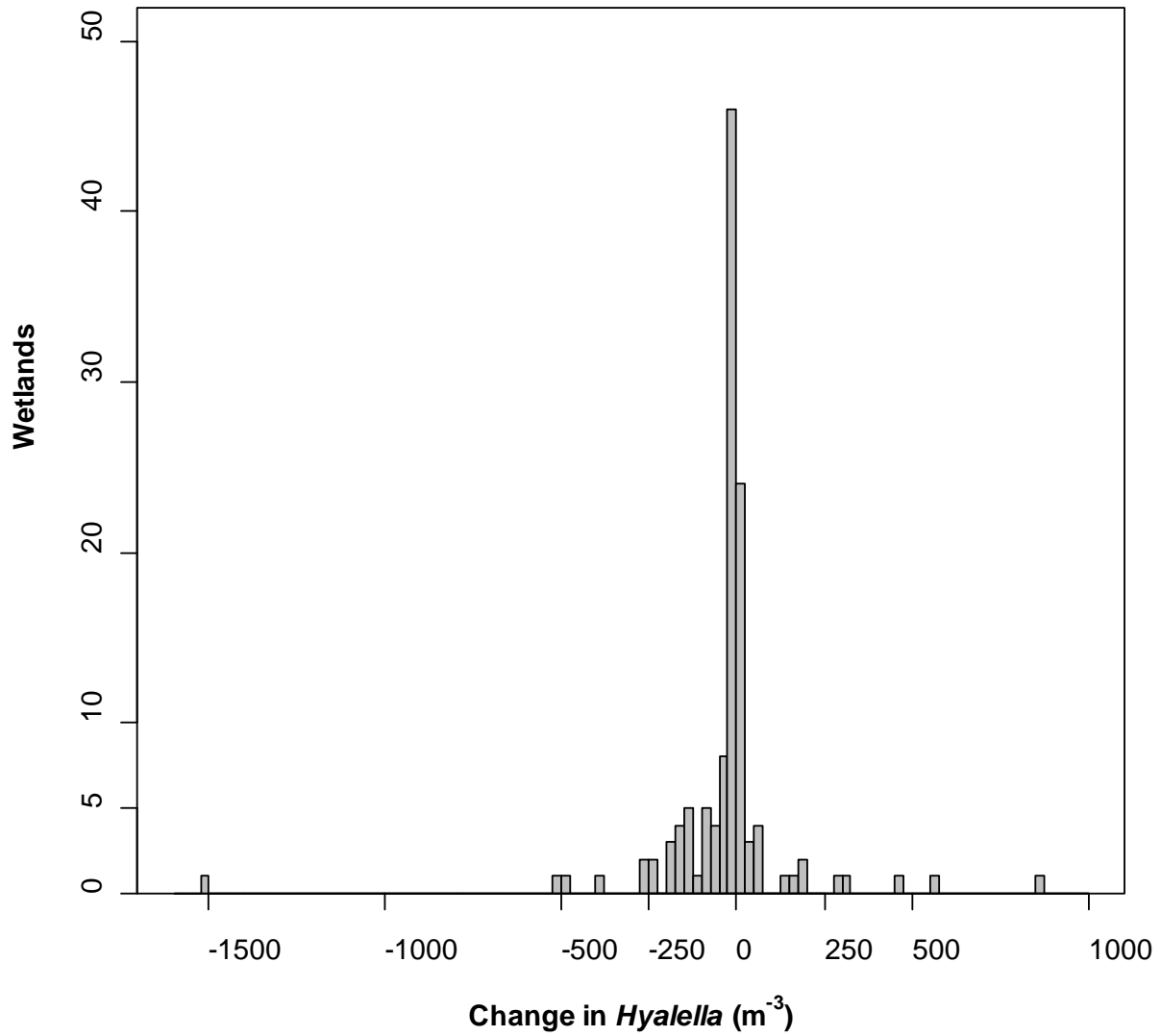


Figure 16. Distribution histogram of change in measured density of *Gammarus lacustris* within 124 semipermanent and permanent prairie pothole wetlands of North Dakota from 2004 or 2005 to 2010.

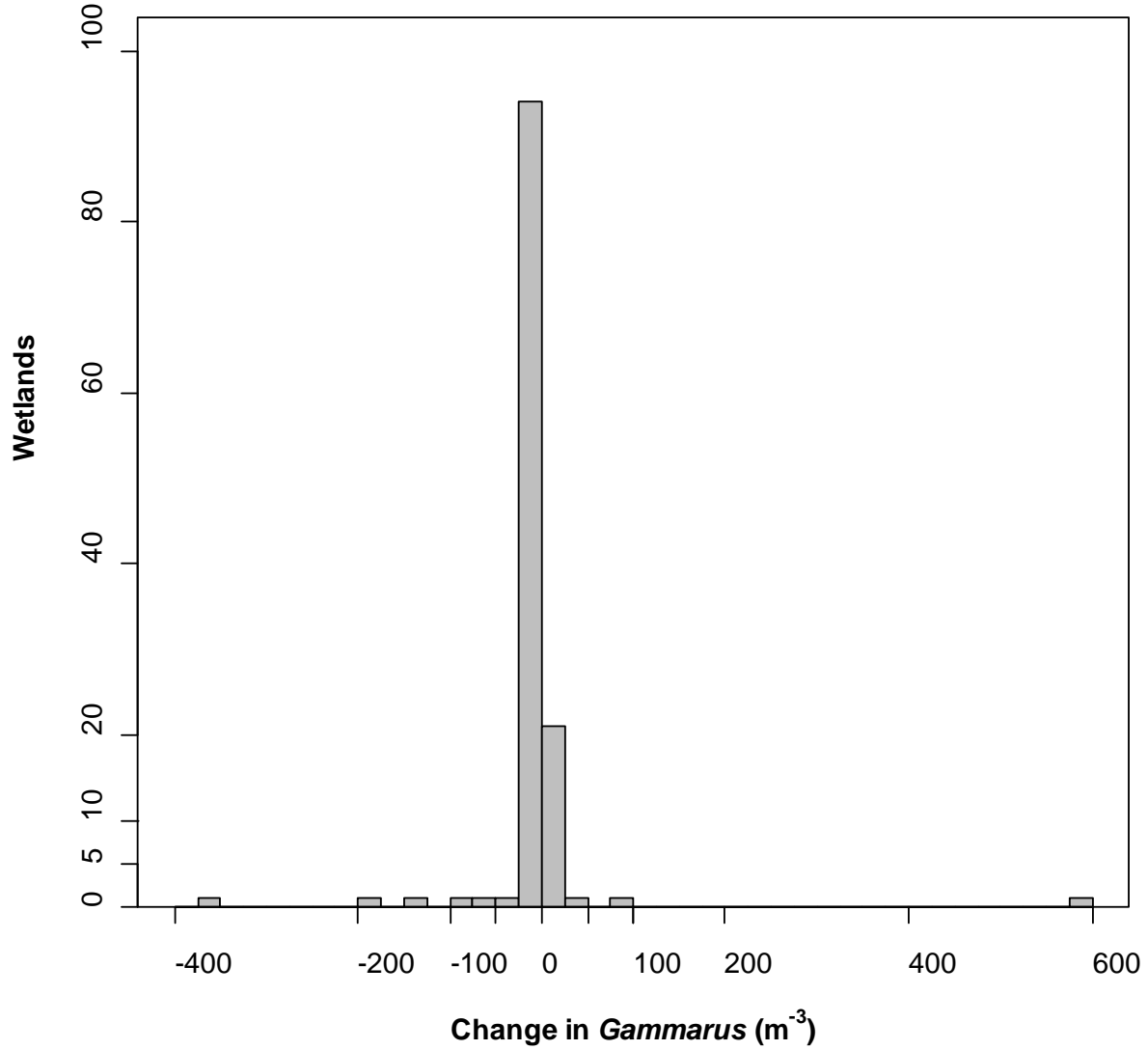


Figure 17. Back-transformed geometric least-squares mean catch per unit effort ( $\pm$  95% CI) of fish groups in springs of 2004 or 2005 (circle; n = 90), and 2011 (triangle; n=131) within semipermanent and permanent prairie pothole wetlands of North Dakota. Fish groups are fathead minnows, Small Fish = other small fish species typically < 10 cm in length, and Large Fish = fish species typically >10 cm in length.

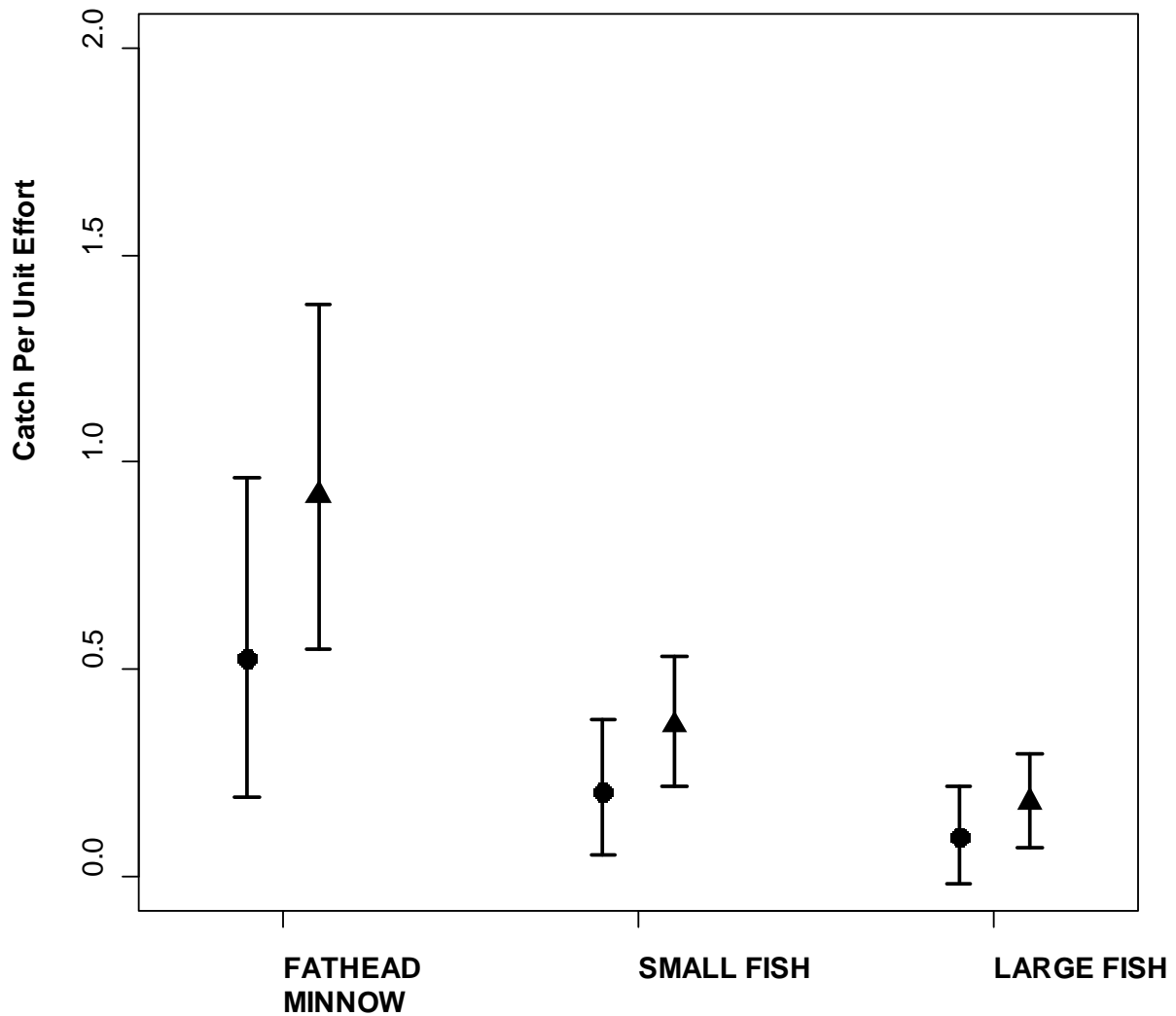


Figure 18. Least-squares estimated mean coverage of wetland by cattail (proportion;  $\pm$  95% CI) in 2011. Regions are depicted as COT = Missouri Coteau, NGP = Northern Glaciated Plains, and RRV = Red River Valley.

