1-1-2004

Impacts of water development on aquatic macroinvertebrates, amphibians, and plants in wetlands of a semi-arid landscape

Ned H. Euliss Jr.
U.S. Geological Survey, ceuliss@usgs.gov

David M. Mushet
U.S. Geological Survey, david_mushet@usgs.gov

Impacts of water development on aquatic macroinvertebrates, amphibians, and plants in wetlands of a semi-arid landscape

Ned H. Euliss, Jr.* and David M. Mushet

U.S. Geological Survey, Northern Prairie Wildlife Research Center, 8711 37th St. SE, Jamestown,
North Dakota, 58401-7317, USA
Corresponding author: (701) 253-5564; E-mail: ned_euliss@usgs.gov

*We compared the macroinvertebrate and amphibian communities of 12 excavated and 12 natural wetlands in western North Dakota, USA, to assess the effects of artificially lengthened hydroperiods on the biotic communities of wetlands in this semi-arid region. Excavated wetlands were much deeper and captured greater volumes of water than natural wetlands. Most excavated wetlands maintained water throughout the study period (May to October 1999), whereas most of the natural wetlands were dry by June. Excavated wetlands were largely unvegetated or contained submergent and deep-marsh plant species. The natural wetlands had two well-defined vegetative zones populated by plant species typical of wet meadows and shallow marshes. Excavated wetlands had a richer aquatic macroinvertebrate community that included several predatory taxa not found in natural wetlands. Taxa adapted to the short hydroperiods of seasonal wetlands were largely absent from excavated wetlands. The amphibian community of natural and excavated wetlands included the boreal chorus frog (*Pseudacris maculata*), northern leopard frog (*Rana pipiens*), plains spadefoot (*Scaphiopus bombifrons*), Woodhouse's toad (*Bufo woodhousii woodhousii*), and tiger salamander (*Ambystoma tigrinum*). The plains spadefoot occurred only in natural wetlands while tiger salamanders occurred in all 12 excavated wetlands and only one natural wetland. Boreal chorus frogs and northern leopard frogs were present in both wetland types; however, they successfully reproduced only in wetlands lacking tiger salamanders. Artificially extending the hydroperiod of wetlands by excavation has greatly influenced the composition of native biotic communities adapted to the naturally short hydroperiods of wetlands in this semi-arid region. The compositional change of the biotic communities can be related to hydrological changes and biotic interactions, especially predation related to excavation.*

Keywords: dugouts, excavation, hydroperiod, impoundments, North Dakota, salamanders

Introduction

Permanent water sources in arid and semi-arid regions are rare because evaporation rates are greater than annual precipitation rates. This lack of permanent water gives seasonal water-bodies in these regions greater ecological significance than in more mesic regions (Williams, 1985) because they are often a limiting resource. The vertebrate and invertebrate communities of seasonal wetlands are composed of unique assemblages of animals that exclude most of the species of more permanent waters (Wiggins et al., 1980). Seasonal wetlands are often considered to be harsh environments because of their short hydroperiods (i.e., the period of time a wetland is flooded) separated by long periods when the wetland is dry. However, harsh environments provide unique opportunities for specially adapted species (Collinson et al., 1995). Productivity is often high in seasonal wetlands due to remineralization of nutrients during the dry period; the shallow waters of seasonal wetlands warm quickly in the spring enabling growth in species with high thermal coefficients; and
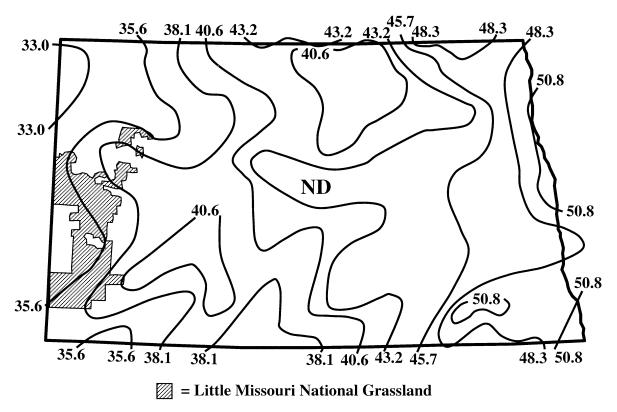
73

Figure 1. Average annual precipitation (cm) in North Dakota, USA, modified from Jensen (1972), and location of the Little Missouri National Grassland.

most large predators are excluded from seasonal wetlands, benefiting many species vulnerable to predation (Collinson et al., 1995). However, because seasonal wetlands are inherently small and shallow, they are very vulnerable to damage by human activities (Collinson et al., 1995; Euliss and Mushet, 1999).

The Little Missouri National Grassland (LMNG) is a 415,000-ha public grassland within an expansive area of natural grassland in western North Dakota, USA, under the management of the U.S. Department of Agriculture's Forest Service (Figure 1). The LMNG and surrounding grasslands are of considerable economic value to the livestock industry, and the area has been extensively modified to enhance the distribution and availability of water resources for livestock. These human-enhanced and developed water sources have enabled ranchers to distribute livestock more evenly throughout the LMNG. Prior to these water developments, livestock were restricted in distribution and grazing pressure was exerted differentially, concentrated around available water sources such as the few permanent wetlands, streams, and springs scattered throughout the area. Recently, the environmental ben-

efits of water developments and improvements within the LMNG have been questioned. Potential environmental concerns range from the effects of hydrologic alterations on aquatic animals and plants in wetlands and streams to impacts on native plant species composition and structure, including related impacts on wildlife that use grasslands.

Water development projects completed over the past several decades in the LMNG have been initiated mostly to enhance water availability for livestock. Stock tanks associated with springs are one of the older types of water developments and are still common. Additionally, earthen stock dams have been constructed in drainages and wetland basins have been excavated to extend the period water is available to livestock. More recently, extensive networks of underground pipelines have been developed that supply water to stock tanks from wells placed within the LMNG. In addition, private and federal conservation agencies have constructed a number of wetlands and shallow impoundments that serve the dual purpose of providing brood-rearing habitat for waterfowl and water for livestock. In all situations, the result has been to put more

water on the landscape than was historically present. Here, we compare the hydroperiod and biotic communities (plants, macroinvertebrates, and amphibians) of natural and excavated palustrine wetlands in the LMNG.

Study area

The topographic features of the LMNG consist of mostly moderate-relief grassland with steeper gradient areas near the Little Missouri River. The erodability of soils in this region is well documented (Bluemle, 2000) and it is the main factor responsible for the physical appearance of the steeper gradient areas, commonly known as 'Badlands.' Average annual precipitation in the LMNG is approximately 38 cm or less (Figure 1). National Wetlands Inventory (NWI) basin coverage for the LMNG identified 2599 palustrine wetlands fully or partially located on federal lands (Table 1). Of these, approximately 21% were identified as having a temporary water regime (i.e., usually go dry in late spring or early summer), 24% as having a seasonal water regime (i.e., usually go dry by mid to late summer), and 55% as having a semipermanent water regime (i.e., only go dry during periods of extended drought). Additionally, 83% of the palustrine wetlands were identified as being altered by dams, excavations, or a combination of the two (Table 1). In fact, the NWI basin coverage identified only 239 temporary wetlands, 184 seasonal wetlands, and 23 semipermanent wetlands on federal lands in the LMNG that have not been altered by impoundment or excavation.

Methods

We limited our sample universe to include only wetlands with seasonal water regimes located entirely on federal land. From these wetlands, we randomly selected 12 wetlands modified by excavations (hereafter referred to as excavated wetlands) and 12 wetlands unmodified by any type of water development (hereafter referred to as natural wetlands). To insure that communities had time to adjust to new ecological conditions, we did not include recently excavated wetlands (i.e., wetlands excavated within the last 6 years) in our sample. To represent wetlands of various sizes in our sample, we arranged all potential study wetlands into four groupings based on wetland size, and randomly assigned a number from 1 to *n* to each wetland within each grouping. We then sorted our list of potential study wetlands by their randomly assigned numbers and selected the first 3 excavated wetlands and the first 3 natural wetlands from each size grouping for a total of 24 wetlands. We assessed the suitability of potential sample wetlands initially with high-altitude aerial photographs supplied by the Custer National Forest followed by inspection by field crews. If any anomalies (e.g., another livestock water source within the wetland basin or catchment) that would preclude a wetland's use in this study were identified, we rejected the site and the next wetland within that size group was selected and evaluated as a potential study site. We repeated this process until 24 wetlands (12 excavated and 12 natural) were selected (Table 2).

We evaluated the hydrology and basin morphometry of study wetlands using monthly (May to October) readings from staff gauges and topographic survey data. During each monthly sampling visit, we recorded the water level and specific conductivity (a proxy for salinity) of each wetland using staff gauges installed in each wetland and an Orion model 126 conductivity meter, respectively. We conducted a detailed topographic survey of each wetland and the adjacent upland using a Nikon, model DTM 750 total station. Topographic data from our total station survey were used to develop three-dimensional models that we used to calculate water volumes and surface areas of wetlands at water levels observed throughout the summer (Tripod Data Systems, 1997).

Table 1. Palustrine wetlands fully or partially on federal lands in the Little Missouri River National Grassland, North Dakota, identified in National Wetland Inventory basin coverage with a diked/impounded modifier, excavated modifier, or both.

Modifier	Water Regime			
	Temporary (n = 534)	Seasonal (n = 624)	Semipermanent (n = 1441)	All (n = 2599)
Diked/Impounded	295	432	1364	2091
Excavated	0	8	53	61
Both	0	0	1	1
% altered	55%	71%	98%	83%

Table 2. Township, Range, and Section (T/R/S); and longitude and latitude of 12 natural (labeled 1N–12N) and 12 excavated (labeled 1E–12E) wetlands sampled in the Little Missouri National Grassland, North Dakota, 1999.

Wetland	T/R/S	Longitude	Latitude
1N	137/100/21	103 17′ 57.6″	46 40′ 12.6″
2N	153/094/06	102 49′ 37.9″	48 06′ 37.4″
3N	147/098/02	103 07′ 36.4″	47 34′ 38.0″
4N	152/097/02	103 03′ 59.3″	48 00′ 33.4″
5N	151/095/22	102 49′ 48.4″	47 52′ 40.4″
6N	153/096/26	102 59′ 11.8″	48 02′ 53.6″
7N	153/096/02	102 59′ 11.3″	48 06′ 02.1″
8N	153/094/06	102 49′ 29.2″	48 06′ 18.4″
9N	153/096/21	103 01′ 19.2″	48 03′ 12.4″
10N	153/095/02	102 51′ 16.3″	48 06′ 34.4″
11N	151/095/21	102 50′ 56.4″	47 53′ 26.3″
12N	153/095/11	102 51′ 59.3″	48 05′ 47.4″
1E	138/100/21	103 18′ 09.3″	46 45′ 23.3″
2E	146/103/10	103 47′ 17.6″	47 28′ 38.7″
3E	134/102/12	103 25′ 38.3″	46 25′ 36.3″
4E	148/103/05	103 50′ 11.7″	47 40′ 12.5″
5E	153/094/21	102 46′ 46.3″	48 03′ 17.3″
6E	148/102/10	103 39′ 55.2″	47 38′ 52.6″
7E	147/103/05	103 50′ 19.9″	47 35′ 10.4″
8E	153/095/09	102 53′ 40.4″	48 05′ 22.8″
9E	148/098/28	103 10′ 45.0″	47 36′ 26.4″
10E	146/103/26	103 45′ 36.2″	47 26′ 36.3″
11E	151/095/35	102 48′ 37.9″	47 51′ 14.2″
12E	153/095/02	102 51′ 28.6″	48 06′ 32.7″

In mid-July, we sampled plant communities by placing two 1 m × 1 m plots (one in the center of the wet-meadow zone and one in the shallow-marsh zone; Stewart and Kantrud, 1971) along randomly placed transects in each wetland. We recorded species composition, percent cover by species (Daubenmire, 1959), and percent unvegetated area within each plot. To facilitate our ability to identify species under intense grazing pressure, we installed two circular cattle exclosures 10 m away from each sample plot. Exclosures were constructed of 1.2 m by 4.9 m commercially available livestock panels with the ends joined together to form a circle approximately 1.5 m in diameter. Each exclosure was held in place by steel T-posts driven into the ground. At each study wetland, we placed one exclosure in the shallow-marsh zone and a second in the wet-meadow zone. Plant specimens collected from exclosures were identified to species using Flora of the Great Plains (Great Plains Flora Association, 1991) and used to aid in the identification of plants exposed to grazing in our plots.

We used sweep nets (Swanson et al., 1974) to collect three aquatic macroinvertebrate samples monthly (May–October) from random locations within each study wetland. The 20.3 cm × 45.7 cm nylon sweep net had 8 meshes per cm with 1 mm apertures. We standardized the horizontal distance covered by each sweep to 61 cm with the aid of a U-shaped rod to provide a sample from 57 l of wetland water. The small sizes of the wetlands and the relatively uniform vegetation within wetlands negated the need to stratify sampling by plant communities. We preserved samples from each sweep in 80% ethanol until we were able to identify taxa and estimate abundance. After we identified and counted each taxon, the samples were archived at the Northern Prairie Wildlife Research Center. We compared taxonomic richness, relative abundance of total and individual taxa, and foraging guild (Merritt and Cummins, 1984) ratios between excavated and natural wetlands using analysis of variance and compositional analysis (Aitchison, 1986).

We sampled amphibians along wetland edges and in the adjacent upland area using visual encounter surveys (VES) (Crump and Scott, 1994) and from within wetlands by seining each month (May–October) with a 15-m minnow seine (6-mm mesh). We standardized the area of each wetland seined by anchoring one end of the seine to a pole located at the wetland edge. We then pulled the other end of the seine to make a 180° arc through the wetland, starting and ending on the shore. We identified larval amphibians to the lowest taxon possible and adults to species or subspecies using Conant and Collins (1991). For each seine sample, we counted the number of individuals of each taxon. We then compared amphibian populations between excavated and natural wetlands.

Results

Excavated wetlands had greater water depths, held greater volumes of water, and had longer hydroperiods than natural wetlands (Table 3). Maximum water depth of all but three excavated wetlands was greater than 1 m when we first sampled in May. The water depth of each wetland gradually decreased throughout the summer, declining by an average of 0.68 m (sd = 0.37 m) by October. Six of the 12 excavated wetlands still had water deeper than 1 m during our last sampling in October; only a single excavated wetland went dry during 1999. Water volumes during May in excavated wetlands ranged from 54 to 2849 m^3 (Table 3). The

Table 3. Water depth, volume, and specific conductance of 12 natural wetlands (labeled 1N to 12N) and 12 excavated wetlands (labeled 1E to 12E) in the Little Missouri National Grassland, North Dakota, May to October 1999.

Wetland	Water Depth (m)						Water Volume (m^3)						Specific Conductance ($\mu S\ cm^{-1}$)					
	May	Jun	Jul	Aug	Sep	Oct	May	Jun	Jul	Aug	Sep	Oct	May	Jun	Jul	Aug	Sep	Oct
1N	0.32	0.12	Dry	Dry	Dry	Dry	51	7	Dry	Dry	Dry	Dry	758	1084	Dry	Dry	Dry	Dry
2N	0.35	Dry	Dry	Dry	Dry	Dry	55	Dry	Dry	Dry	Dry	Dry	39	Dry	Dry	Dry	Dry	Dry
3N	0.52	0.36	Dry	Dry	Dry	Dry	73	33	Dry	Dry	Dry	Dry	158	203	Dry	Dry	Dry	Dry
4N	0.23	Dry	Dry	Dry	Dry	Dry	11	Dry	Dry	Dry	Dry	Dry	62	Dry	Dry	Dry	Dry	Dry
5N	0.57	0.43	0.27	Dry	Dry	Dry	370	235	113	Dry	Dry	Dry	96	113	81	Dry	Dry	Dry
6N	0.14	Dry	Dry	Dry	Dry	Dry	3	Dry	Dry	Dry	Dry	Dry	63	Dry	Dry	Dry	Dry	Dry
7N	0.22	Dry	Dry	Dry	Dry	Dry	13	Dry	Dry	Dry	Dry	Dry	65	Dry	Dry	Dry	Dry	Dry
8N	0.21	Dry	Dry	Dry	Dry	Dry	54	Dry	Dry	Dry	Dry	Dry	28	Dry	Dry	Dry	Dry	Dry
9N	0.31	0.20	0.20	Dry	Dry	Dry	47	12	13	Dry	Dry	Dry	494	1282	1572	Dry	Dry	Dry
10N	0.33	Dry	Dry	Dry	Dry	Dry	40	Dry	Dry	Dry	Dry	Dry	49	Dry	Dry	Dry	Dry	Dry
11N	0.42	Dry	Dry	Dry	Dry	Dry	170	Dry	Dry	Dry	Dry	Dry	637	Dry	Dry	Dry	Dry	Dry
12N	0.19	Dry	Dry	0.02	0.13	0.06	90	Dry	Dry	1	41	5	43	Dry	Dry	295	385	670
1E	0.77	0.71	0.59	0.56	0.54	0.48	395	332	224	198	191	150	2800	3900	5100	4730	4990	7350
2E	2.41	2.25	2.15	1.86	2.12	2.03	2849	2310	2021	1327	1934	1686	239	392	264	310	378	431
3E	1.41	1.41	1.07	0.96	0.90	0.82	443	443	238	190	164	134	253	184	257	276	350	313
4E	0.81	0.79	0.66	0.52	0.43	0.36	289	274	196	118	82	57	175	199	172	208	236	314
5E	0.36	0.07	0.24	Dry	Dry	Dry	54	2	23	Dry	Dry	Dry	166	384	603	Dry	Dry	Dry
6E	1.95	1.97	1.76	1.56	1.30	1.20	724	739	550	408	273	229	271	275	213	332	297	394
7E	1.99	2.06	1.81	1.64	1.52	1.42	1219	1313	1008	803	674	574	448	349	510	450	475	604
8E	2.15	1.90	1.71	1.48	1.30	1.15	1282	1003	809	609	476	383	180	234	215	214	168	213
9E	2.36	2.08	2.08	1.81	1.56	1.44	2815	1959	1975	1376	965	809	115	159	223	179	175	307
10E	1.21	1.12	1.17	1.01	0.80	0.72	112	939	1047	755	464	375	276	329	392	586	742	923
11E	2.39	1.85	1.25	0.92	0.85	0.78	1346	592	227	116	98	82	305	394	321	372	440	564
12E	2.00	1.70	1.43	1.69	1.48	1.27	544	325	209	321	227	160	72	173	212	167	195	228

77

average volume of water retained in excavated wetlands ranged from 1006 m^3 (sd = 959 m^3) in May to 387 m^3 (sd = 472 m^3) by October. In contrast, all 12 natural wetlands had a maximum water depth less than 1 m in May and most (8 of 12) were dry on our second visit in June; all 12 wetlands were dry by August. One natural wetland, dry in June and July, refilled by August from isolated thundershowers and contained standing water through our October sampling period. Water volume in the natural wetlands in May ranged from 3 to 370 m^3. The average volume of water held in the natural wetlands in May was 81 m^3 (sd = 101 m^3).

In addition to being deeper and containing greater volumes of water, excavated wetlands also had higher concentrations of dissolved salts than natural wetlands (Table 3). Specific conductance readings in May in all but one excavated wetland were greater than 100 μS cm^{-1}. In contrast, only four natural wetlands had specific conductance values greater than 100 μS cm^{-1}. Specific conductance of wetlands increased seasonally in response to water loss from evapotranspiration. One excavated wetland (1E, Table 3) had higher specific conductance than other wetlands that appeared to result from extremely salty groundwater entering the basin from groundwater seeps around the basin's periphery.

Our survey data suggest that the plant communities of natural and excavated wetlands are very different. We observed 64 plant species in our study wetlands. Twelve species were common to both excavated and natural wetlands, while 22 species were found only in excavated wetlands and 30 were found only in natural wetlands. Many wet-meadow and shallow-marsh plant species (Stewart and Kantrud, 1971) were conspicuously absent from the excavated wetlands but were found in natural wetlands. These species included needle spikerush (*Eleocharis acicularis*), common spikerush (*Eleocharis macrostachya*), baltic rush (*Juncus balticus*), and several sedge species (*Carex* spp.). Additionally, submergent species such as pale watermilfoil (*Myriophyllum spicatum*), sago pondweed (*Potamogeton pectinatus*), baby pondweed (*Potamogeton pusillus*), and claspingleaf pondweed (*Potamogeton richardsonii*), and the deep-marsh emergent hardstem bulrush (*Scirpus acutus*) were absent from the natural wetlands. Of special significance was the difference in the percentage of unvegetated area between excavated and natural wetlands. Eight of the 12 excavated wetlands lacked vegetation in greater than 90% of the area in our shallow-marsh plots; four excavated wetlands did not have any visible vegetation inward from the wet-meadow zone. In contrast, only four of the 12 natural wetlands had unvegetated area in our shallow-marsh plots.

The number of aquatic macroinvertebrate taxa we observed in each wetland from May until October, 1999, differed between excavated and natural wetlands (F$_{1,22}$ = 13.22, P = 0.0015). We observed an average of 35.3 (SE = 3.0) taxa in excavated wetlands and only 20.1 (SE = 3.0) taxa in natural wetlands. Eight natural wetlands had 21 or fewer taxa while all 12 excavated wetlands had greater than 21 taxa (Figure 2). We did not identify any significant differences in foraging guild composition between excavated and natural wetlands (λ = 0.706, F$_{5,18}$ = 1.50, P = 0.2385). However, some taxa such as the mosquito *Aedes*, the fairy shrimp *Eubranchipus*, and the snails *Promenetus umbilicatellus* and *Stagnicola caparata* occurred only in the natural wetlands. The leeches *Erpodella* and *Helobdella*, the damselfly *Enallagma*, the dragonfly *Aeshna*, and the pill clams *Sphaerium lacustre, Pisidium casertanum*, and *Pisidium compressum* occurred only in the excavated wetlands.

We observed the boreal chorus frog (*Pseudacris maculata*), northern leopard frog (*Rana pipiens*), plains spadefoot (*Scaphiopus bombifrons*), Woodhouse's toad (*Bufo woodhousii woodhousii*), and tiger salamander (*Ambystoma tigrinum*) in our survey of excavated and natural wetlands in the LMNG. We also encountered the plains garter snake (*Thamnophis radix*) and the bullsnake (*Pituophis melanoleucus sayi*). While adult boreal chorus frogs and northern leopard frogs were present in almost all wetlands in the spring, they only successfully reproduced (i.e., we observed tadpoles) in wetlands that were void of tiger salamanders. We encountered tiger salamanders in all 12 excavated wetlands, but in just a single natural wetland (Figure 3); the observation in the natural wetland was represented by a single adult. The plains spadefoot occurred only in 3 wetlands, all of which were natural. We encountered the Woodhouse's toad, plains garter snake, and bullsnake infrequently around the edges of both excavated and natural wetlands.

Discussion

Our data indicate that seasonal wetlands in the LMNG have been substantially altered by excavation. Consistent with their design and objectives, excavated wetlands ponded more and possessed deeper water, and contained water for longer periods than natural wetlands. However, in addition to providing a more reliable water source for livestock, these changes have
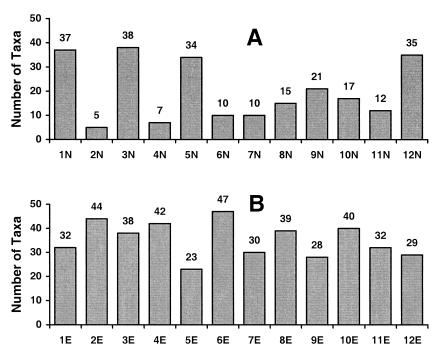
Figure 2. Number of aquatic macroinvertebrate taxa observed in 12 natural (A) and 12 excavated (B) wetlands in the Little Missouri National Grassland, North Dakota, May–October 1999.

significantly impacted the native plant and animal communities of wetlands in the LMNG. The impact of hydrologic alterations alone is sufficient to change the aquatic invertebrate composition (Euliss et al., 1999) and data from our study suggest significant alteration in the plant and amphibian community as well.

Excavation has greatly altered the plant community of wetlands in the LMNG. The natural wetlands had two well-defined plant zones populated by typical wet-meadow and shallow-marsh species, whereas the excavated wetlands were largely unvegetated or contained submergent and deep-marsh plant species typical of the deeper waters and extended hydroperiods resulting from excavation. Vegetative structure has a significant influence on aquatic macroinvertebrate communities (Euliss et al., 1999). Macrophytes increase habitat structural complexity within wetlands, providing food and living space for species that would not otherwise be present (e.g., Berg, 1949, 1950; Krull, 1970; Gilinsky, 1984; Bergey et al., 1992). They also function as sites for oviposition (Sawchyn and Gillott, 1974a, b, 1975), emergence (Sawchyn and Gillott, 1974a, b), respiration (Batzer and Sjogren, 1986), attachment (Campbell et al., 1982), and pupation (Butcher, 1930) and can modify predator-prey interactions in wetlands (e.g., Rabe and Gibson, 1984; Gilinsky, 1984; Batzer and Resh, 1991).

Additionally, aquatic plants can alter the physical and chemical environment of the water. Aquatic plants influence water circulation patterns and contribute to gradients in light, temperature, and dissolved oxygen (e.g., Kollman and Wali, 1976; Carpenter and Lodge, 1986; Rose and Crumpton, 1996). Further, anoxic conditions that can impact macroinvertebrate abundance, movement, and behavior (e.g., Murkin and Kadlec, 1986; Murkin et al., 1992) can also be altered by stands of emergent vegetation (Suthers and Gee, 1986; Rose and Crumpton, 1996). All of these factors interact to result in different macroinvertebrate communities often being associated with different plant communities (e.g., Voigts, 1976; McCrady et al., 1986; Wrubleski, 1987; Olsen et al., 1995).

In addition to vegetative composition, hydroperiod also directly influences the invertebrate community of wetlands. In order to persist in temporary and seasonal wetlands, aquatic macroinvertebrate species must possess two essential life cycle adaptations: an ability to withstand the period when the wetland is dry and an ability to synchronize life cycles with the occurrence of water (Williams, 1985). Wiggins et al. (1980) placed animal inhabitants of seasonal waters into four groups based on these lifecycle adaptations:

	May	June	July	Aug.	Sept.	Oct.
1N			dry	dry	dry	dry
2N		dry	dry	dry	dry	dry
3N			dry	dry	dry	dry
4N		dry	dry	dry	dry	dry
5N				dry	dry	dry
6N		dry	dry	dry	dry	dry
7N		dry	dry	dry	dry	dry
8N		dry	dry	dry	dry	dry
9N				dry	dry	dry
10N		dry	dry	dry	dry	dry
11N		dry	dry	dry	dry	dry
12N		dry	dry			
1E						
2E						
3E						
4E						
5E				dry	dry	dry
6E						
7E						
8E						
9E						
10E						
11E						
12E						

Figure 3. Natural wetlands (labeled 1N to 12N) and excavated wetlands (labeled 1E to 12E) in the Little Missouri National Grassland, North Dakota, in which tiger salamanders (*Ambystoma tigrinum*) were captured in seine samples, May to October 1999. Shading indicates time periods when wetlands contained water.

Group I. Overwintering Residents. These permanent residents are incapable of active dispersal. They exist in a dormant state during dry periods as drought-resistant cysts and eggs or as juveniles and adults.

Group II. Overwintering Spring Recruits. These overwinter in the dry basin mainly as eggs or larvae but actively disperse in the spring.

Group III. Overwintering Summer Recruits. These active dispersers are not dependent on the presence of surface water for reproduction. Oviposition occurs in the dry wetland basin and they overwinter mainly in the egg stage or as larvae.

Group IV. Non-wintering Spring Migrants. These active dispersers enter seasonal pools in the spring but

must leave the pool before it dries, overwintering mainly in permanent waters.

Given the potential pool of Group I, II, III, and IV macroinvertebrates in the LMNG, hydroperiod is the primary factor influencing aquatic communities in freshwater wetlands. Schneider (1999) presents a model of community organization for wetland invertebrates that demonstrates how pond duration acts as a filter; only taxa with life history strategies compatible with pond duration are able to pass through the filter and inhabit the pond. Invertebrates with long life cycles such as dragonflies and predaceous diving beetles are filtered out and are unable to exist in the shortest hydroperiod wetlands. However, as hydroperiod lengthens, the filter becomes more porous and an increasing number of aquatic invertebrates can occupy the wetland. In our study, we observed that excavated wetlands had the greatest richness of aquatic macroinvertebrate taxa (Figure 2). It is important to note that while short-hydroperiod wetlands may support relatively fewer aquatic invertebrates, it does not mean that they are species poor for the entire annual cycle. Terrestrial invertebrates may be a significant component of the fauna of seasonal wetlands during the dry phase (Collinson et al., 1995).

While we did not detect any significant differences in the foraging guild ratios, we encountered several predatory taxa (e.g., the leeches *Erpodella* and *Helobdella*, the damselfly *Enallagma*, and the dragonfly *Aeshna*) only in excavated wetlands. Other non-predatory taxa also occurred only in the excavated wetlands likely due to the artificially lengthened hydroperiods. Schneider and Frost (1996) found that predators from long-hydroperiod ponds fed preferentially on prey taxa such as *Aedes* mosquitoes and the fairy shrimp *Eubranchipus* that are most characteristic of short hydroperiod ponds. *Aedes* and *Eubranchipus* were not observed in the excavated wetlands we sampled.

While our data demonstrates several impacts of excavation on wetland invertebrates, there are likely additional impacts hidden in the coarse taxonomic resolution of our evaluation. We rarely identified individuals to species and usually only to genera or family. One exception was for the gastropods, which we identified to species. Of the eight snail species, only one (*Gyralus circumstriatus*) occurred in both excavated and natural wetlands. *Gyralus parvus*, *Helisoma trivolvis*, *Physa gyrina*, *Physa jennessi*, and *Stagnicola elodes* occurred only in excavated wetlands while *Stagnicola caparata* and *Promenetus umbilicatellus* occurred only in natural wetlands. At the genera level, we would have shown

Stagnicola as occurring at equal frequencies in both excavated (3) and natural (3) wetlands. Other macroinvertebrate groups likely had many more species represented by just a single genus or family. A more detailed assessment to a finer taxonomic resolution will likely reveal that other invertebrates adapted to short hydroperiod wetlands have been negatively affected by excavation.

Animal species adapted to survive in seasonal waters are often rare with a restricted distribution. Clarke (1981) describes *Promenentus umbilicatellus* as being rather uncommon, restricted to vernal pools, marshes, and spring-time flooded margins of intermittent streams. The Eubranchiopoda (which includes the fairy, tadpole, and clam shrimps) are among the most characteristic inhabitants of seasonal ponds and pools (Pennak, 1989). While some Eubranchiopoda are widely occurring, many are quite restricted, and some are only known from a single pool or pond (Pennak, 1989). Currently, five species of fairy shrimp are listed on the federal list of threatened or endangered species (U.S. Fish and Wildlife Service, 2001). Given the often restricted nature of aquatic invertebrates adapted to survive in seasonal waters and their vulnerability to increases in predatory and competitive pressures, care should be taken to avoid artificially extending the hydroperiods of wetlands in semi-arid regions. Additional consideration should be given to restoring natural hydroperiods in altered wetlands where possible.

Semlitsch (2000) provides a checklist of questions useful in developing biologically based management plans for amphibian communities. The first two questions Semlitsch poses are: 1) "What species currently inhabit your region?" and 2) "What was the historical species richness and relative abundance of amphibians in your region?" While the first question can be easily answered, the second is more difficult, but it is of special significance to amphibians in the LMNG. While we do not know the historical species richness and abundance of amphibians in the LMNG, it is clear that the hydroperiods of most wetlands are inherently short. Amphibian species existing in the seasonal waters of LMNG wetlands likely possessed physiological tolerances and life histories compatible with the hydrology of this semi-arid region. The larval period of spadefoot toads, which can be as short as 21 days (Semlitsch, 2000), is an example of a life history adaptation allowing this species to capitalize on the short hydroperiods of wetlands in the region. Spadefoot toad tadpoles are extremely vulnerable to predatory insects and salamanders. Thus, they are dependent on wetlands with hydroperiods too short to support predatory populations (Pechmann et al., 1989).

By contrast, the tiger salamander can produce metamorphs only in wetlands that do not dry for at least 3 to 4 months (Semlitsch, 1983). Because both adult and larval tiger salamanders are carnivorous and frequently occur at high densities, they can exert considerable predation pressure on other amphibian species (Morin, 1981). Regulation of amphibian community structure in wetlands occurs through the interaction of hydroperiod, competition and predation (Wellborn et al., 1996); changes to any of these three factors will result in changes to the community structure. The increase in hydroperiods of most wetlands in the LMNG now allows tiger salamanders and predatory insects to exert pressure on anuran tadpoles at levels that did not previously exist.

Historically, wetlands with hydroperiods long enough to support tiger salamander populations were scarce in the LMNG. However, current NWI basin coverage data identified that over half (1441) of the 2599 palustrine wetlands fully or partially on federal lands in the LMNG currently have semipermanent water regimes (Table 1). NWI also identified that 98% (1418) of these basins have been altered by excavations and/or dams to extend their hydroperiods. Historically, most of these wetlands would likely have had temporary or seasonal water regimes consistent with the precipitation events that characterize this semi-arid region. Additionally, of the LMNG temporary and seasonal wetlands identified by NWI (Table 1), 55% and 71%, respectively, have been altered to increase hydroperiods through excavation or impoundment. This shift from a landscape dominated by rangeland interspersed with isolated temporary and seasonal wetlands, and very few semipermanent or permanent water sources, to one in which most wetlands have semipermanent water regimes likely had a negative influence on native amphibian populations.

We observed an apparent range extension of the barred subspecies of the tiger salamander (*Ambystoma tigrinum mavortium*) in the LMNG. Current range maps show the blotched tiger salamander (*Ambystoma tigrinum melanostictum*) as being the subspecies occurring throughout most of South Dakota and in southwestern North Dakota with the barred tiger salamander occurring only as far north as northern Nebraska (Conant and Collins, 1991). However, we encountered both barred and blotched tiger salamanders in the LMNG wetlands. While the reasons for this apparent range expansion are unclear, we hypothesize that the creation of numerous wetland habitats suitable for colonization by salamanders across what were historically unfragmented grasslands inhospitable to

salamanders may have allowed these two subspecies to intermix. In addition to the numerous wetlands altered and created in North Dakota, over 70,000 retention and pit-retention reservoirs have been created in western South Dakota (Ruwaldt et al., 1979) that may have provided a suitable habitat corridor from Nebraska. In addition, transportation of barred tiger salamanders as bait for sport fishermen may have greatly increased the dispersal rate of this subspecies. Thus, while the natural isolation of permanent water sources in dry landscapes can promote the genetic divergence of populations (Thomas et al., 1998), reduction in this isolation through the creation of additional permanent water bodies can lead to the intermixing of these once isolated populations.

It is not surprising that when the LMNG was first settled by Europeans, grazing was identified as the principal land use. Nor is it surprising that ranchers have enhanced water availability to livestock in this semi-arid region. Excavation of short hydroperiod wetlands has been a common method of enhancing water availability in the LMNG for livestock because it is cost effective. More recently the benefits of wetlands in southwestern North Dakota to waterfowl have been used to promote the creation and alteration of additional wetlands. Currently, there is a wildlife program to create over 4000 ha of wetlands in southwestern North Dakota for the mutual benefit of wildlife and livestock (Willis, 2001). The benefits of putting additional water on the landscape in semi-arid regions for waterfowl are well documented (Bue et al., 1964; Lokemoen, 1973; Forman et al., 1996). However, as we found for excavated wetlands, such actions can have significant impacts on native aquatic macroinvertebrate, amphibian, and plant communities. The changes we observed were largely the result of deeper water depths, increased hydroperiods, increased salt concentrations, decreased vegetative structure, and the presence of a diverse assemblage of predatory macroinvertebrates and salamanders in excavated wetlands. Populations of species vulnerable to the changes we documented need to be identified for periodic status assessment, and programs need to be developed to restore the natural hydroperiods and biotic communities of wetlands to increase the availability of these unique habitat types in the LMNG.

Acknowledgments

References

Aitchison, J., 1986. *The Statistical Analysis of Compositional Data*. Chapman and Hall, New York, NY, USA.

Batzer, D. P., Resh, V. H., 1991. Trophic interactions among a beetle predator, a chironomid grazer, and periphyton in a seasonal wetland. Oikos 60, 251–257.

Batzer, D. P., Sjogren, R. D., 1986. Larval habitat characteristics of *Coquillettidia perturbans* (Diptera: Culicidae) in Minnesota. Can. Entomol. 118, 1193–1198.

Berg, C. O., 1949. Limnological relations of insects to plants of the genus *Potamogeton*. Trans. Amer. Microscop. Soc. 68, 279–291.

Berg, C. O., 1950. Biology of certain Chironomidae reared from *Potamogeton*. Ecol. Monographs 20, 83–101.

Bergey, E. A., Balling, S. F., Collins, J. N., Lamberti, G. A., Resh, V. H., 1992. Bionomics of invertebrates within an extensive *Potamogeton pectinatus* bed of a California marsh. Hydrobiologia 234, 15–24.

Bluemle, J. P., 2000. *The Face of North Dakota, 3rd Edition*. North Dakota Geological Survey, Bismarck, ND, USA.

Bue, I. G., Uhlig, H. G., Smith, J. D., 1964. Stock ponds and dugouts. In: J. P Linduska (Ed.), *Waterfowl Tomorrow*, pp. 391–398. U.S. Department of the Interior, Fish and Wildlife Service, Washington, DC, USA.

Butcher, F. G., 1930. Notes on the cocooning habits of *Gyrinus*. J. Kansas Entomol. Soc. 3, 64–66.

Campbell, J. M., Clark, W. J., Kosinski, R., 1982. A technique for examining microscopic distribution of Cladocera associated with shallow water macrophytes. Hydrobiologia 97, 225–232.

Carpenter, S. R., Lodge, D. M., 1986. Effects of submersed macrophytes on ecosystem processes. Aquat. Bot. 26, 341–370.

Clark, A. H., 1981. *The Freshwater Molluscs of Canada*. National Museum of Natural Sciences, National Museums of Canada, Ottawa, Canada.

Collinson, N. H., Biggs, J., Corfield, A., Hodson, M. J., Walker, D., Whitfield, M., Williams, P. J., 1995. Temporary and permanent ponds: An assessment of the effects of drying out on the conservation value of aquatic macroinvertebrate communities. Biolog. Conserv. 74, 125–133.

Conant, R., Collins, J. T., 1991. *A Field Guide to Reptiles and Amphibians: Eastern and Central North America, Third Edition*. Houghton Mifflin Company, Boston, MA, USA.

Crump, M. L., Scott, N. J., Jr., 1994. Visual encounter surveys. In: W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L-A. C. Hayek, M. S. Foster (Eds.), *Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians*, pp. 84–92. Smithsonian Institution Press, Washington, DC, USA.

Daubenmire, R. F., 1959. *Plants and environment*. John Wiley & Sons, Inc., New York, NY, USA.

Euliss, N. H., Jr., Mushet, D. M., 1999. Influence of agriculture on aquatic invertebrate communities of temporary wetlands in the prairie pothole region of North Dakota, USA. Wetlands 19, 578–583.

Euliss, N. H., Jr., Wrubleski, D. A., Mushet, D. M., 1999. Wetlands of the prairie pothole region: Invertebrate species composition, ecology, and management. In: D. P. Batzer, R. B. Rader, S. A. Wissinger (Eds.), *Invertebrates in Freshwater Wetlands of North America*, pp. 471–514. John Wiley & Sons, Inc., New York, NY, USA.

Forman, K. J., Madsen, C. R., Hogan, M. J., 1996. Creating multiple purpose wetlands to enhance livestock grazing distribution, range condition, and waterfowl production in western South Dakota. In: J. Schaack, S. S. Anderson (Eds.), *Water for Agriculture and Wildlife and the Environment: Win-Win Opportunities*, pp. 185–192. U. S. Committee on Irrigation and Drainage, Denver, CO, USA.

Gilinsky, E., 1984. The role of fish predation and spatial heterogeneity in determining benthic community structure. Ecology 65, 455–468.

Great Plains Flora Association, 1991. *Flora of the Great Plains*. University Press of Kansas, Lawrence, KS, USA.

Jensen, R. E., 1972. *Climate of North Dakota*. North Dakota State Water Commission, Bismarck, ND, USA.

Kollman, A. L., Wali, M. K., 1976. Intraseasonal variations in environmental and productivity relations of *Potamogeton pectinatus* communities. Archiv für Hydrobiologie, Supplement 50, 439–472.

Krull, J. N., 1970. Aquatic plant-macroinvertebrate associations and waterfowl. J. Wildlife Manage. 34, 707–718.

Lokemoen, J. T., 1973. Waterfowl production on stock-watering ponds in the northern plains. J. Range Manage. 26, 179–184.

McCrady, J. W., Wentz, W. A., Linder, R. L., 1986. Plants and invertebrates in a prairie wetland during duck brood-rearing. Prairie Naturalist 18, 23–32.

Merritt, R. W., Cummins, K. W., 1984. *An Introduction to the Aquatic Insects of North America.* Kendall/Hunt Publishing Company, Dubuque, IA, USA.

Morin, P. J., 1981. Predatory salamanders reverse the outcome of competition among three species of anuran tadpoles. Science 212, 1284–1286.

Murkin, E. J., Murkin, H. R., Titman, R. D., 1992. Nektonic invertebrate abundance and distribution at the emergent vegetation-open water interface in the Delta Marsh, Manitoba, Canada. Wetlands 12, 45–52.

Murkin, H. R., Kadlec, J. A., 1986. Responses by benthic macroinvertebrates to prolonged flooding of marsh habitat. Can. J. Zool. 64, 65–72.

Olson, E. J., Engstrom, E. S., Doeringsfeld, M. R., Bellig, R., 1995. Abundance and distribution of macroinvertebrates in relation to macrophyte communities in a prairie marsh, Swan Lake, Minnesota. J. Freshwat. Ecol. 10, 325–335.

Pechmann, J. H. K., Scott, D. E., Gibbons, J. W., Semlitsch, R. D., 1989. Influence of wetland hydroperiod on diversity and abundance of metamorphosing juvenile amphibians. Wetlands Ecol. and Manage. 1, 3–11.

Pennak, R. W., 1989. *Fresh-water Invertebrates of the United States: Protozoa to Mollusca, Third Edition*. John Wiley & Sons, Inc., New York, NY, USA.

Rabe, F. W., Gibson, F., 1984. The effect of macrophyte removal on the distribution of selected invertebrates in a littoral environment. J. Freshwat. Ecol. 2, 359–370.

Rose, C., Crumpton, W. G., 1996. Effects of emergent macrophytes on dissolved oxygen dynamics in a prairie pothole wetland. Wetlands 16, 495–502.

Ruwaldt, J. J., Flake, L. D., Gates, J. M., 1979. Waterfowl pair use of natural and man-made wetlands in South Dakota. J. Wildlife Manage. 43, 375–383.

Sawchyn, W. W., Gillott, C., 1974a. The life histories of three species of *Lestes* (Odonata: Zygoptera) in Saskatchewan. Can. Entomol. 106, 1283–1293.

Sawchyn, W. W., Gillott, C., 1974b. The life history of *Lestes congener* (Odonata: Zygoptera) on the Canadian prairies. Can. Entomol. 106, 367–376.

Sawchyn, W. W., Gillott, C., 1975. The biology of two related species of coenagrionid dragonflies (Odonata: Zygoptera) in western Canada. Can. Entomol. 107, 119–128.

Schneider, D. W., 1999. Snowmelt pond in Wisconsin: Influence of hydroperiod on invertebrate community structure. In: D. P. Batzer, R. B. Rader, S. A. Wissinger (Eds.), *Invertebrates in Freshwater Wetlands of North America*, pp. 299–318. John Wiley & Sons, Inc., New York, NY, USA.

Schneider, D. W., Frost, T. M., 1996. Habitat duration and community structure in temporary ponds. J. N. Amer. Bentholog. Soc. 15, 64–86.

Semlitsch, R. D., 1983. Structure and dynamics of two breeding populations of the eastern tiger salamander, *Ambystoma tigrinum*. Copeia 1983, 608–616.

Semlitsch, R. D., 2000. Principles for management of aquatic breeding amphibians. J. Wildlife Manage. 64, 615–631.

Stewart, R. E., Kantrud, H. A., 1971. Classification of natural ponds and lakes in the glaciated prairie region. U. S. Department of the Interior, Fish and Wildlife Service, Resource Publication 92. Washington, DC, USA.

Suthers, I. M., Gee, J. H., 1986. Role of hypoxia in limiting diel spring and summer distribution of juvenile yellow perch (*Perca flavescens*) in a prairie marsh. Can. J. Fish. and Aquat. Sci. 43, 1562–1570.

Swanson, G. A., Meyer, M. I., Serie, J. R., 1974. Feeding ecology of breeding blue-winged teals. J. Wildlife Manage. 38, 396–407.

Thomas, E. P., Blinn, D. W., Keim, P., 1998. Do xeric landscapes increase genetic divergence in aquatic ecosystems? Freshwat. Biol. 40, 587–593.

Tripod Data Systems, 1997. *Foresight for Windows 95/NT*. Tripod Data Systems, Inc., Corvallis, OR, USA.

U. S. Fish and Wildlife Service, 2001. Species Information: Threatened and Endangered Animals and Plants (http://endangered. fws. gov/wildlife. html#Species). U. S. Department of the Interior, Fish and Wildife Service, Endangered Species Program. Washington, DC, USA. Date Accessed 10/19/01.

Voigts, D. K., 1976. Aquatic invertebrate abundance in relation to changing marsh vegetation. Amer. Mid. Nat. 95, 313–322.

Wellborn, G. A., Skelly, D. K., Werner, E. E., 1996. Mechanisms creating community structure across a freshwater habitat gradient. Ann. Rev. of Ecol. and Systemat. 27, 337–363.

Wiggins, G. B., Mackay, R. J., Smith, I. M., 1980. Evolutionary and ecological strategies of animals in annual temporary pools. Archiv für Hydrobiologie, Supplement 58, 97–206.

Williams, W. D., 1985. Biotic adaptations in temporary lentic waters, with special reference to those in semi-arid and arid regions. Hydrobiologia 125, 85–110.

Willis, K., 2001. 73 new wetlands created in southwestern North Dakota. Birdscapes 2001(Fall), 12.

Wrubleski, D. A., 1987. Chironomidae (Diptera) of peatlands and marshes in Canada. Mem. Entomol. Soc. Can. 140, 141–161.