Chapter 5
Aquatic Invertebrates of Prairie Wetlands: Community Composition, Ecological Roles, and Impacts of Agriculture

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Abstract. The southern portions of Manitoba, Saskatchewan, and Alberta are covered with millions of small water-filled depressions called prairie potholes. These wetlands provide habitat for a diverse array of aquatic invertebrates, which provide an important food resource for the abundant fauna that use these wetlands. Other functions and values of the aquatic invertebrates are not as well known. More information is needed on taxonomic composition and basic ecology so that we can better understand their role in the wetland trophic dynamics and wetland functioning. This information would also help us to better understand the factors that regulate community composition and abundance, and how agriculture and other anthropogenic impacts are contributing to losses of wetland biodiversity and functioning.

Résumé. Les portions méridionales du Manitoba, de la Saskatchewan et de l'Alberta sont recouvertes de millions de petites dépressions remplies d'eau qu'on l'on appelle fondrières des Prairies. Ces milieux humides accueillent une diversité d'invertébrés aquatiques qui constituent une source importante de nourriture pour de nombreux animaux sauvages. Les autres fonctions et utilités de ces invertébrés aquatiques sont moins bien connues. Nous avons besoin d'en savoir plus sur la composition taxonomique et l'écologie fondamentale de ces organismes afin de mieux comprendre leur rôle dans la dynamique trophique et le fonctionnement des milieux humides. Ce genre d'information nous permettrait également de mieux connaître les facteurs qui assurent la régulation de la composition des communautés et de leur abondance, et les incidences de l'agriculture et des autres facteurs anthropiques sur la réduction de la biodiversité des milieux humides et sur le fonctionnement de ces milieux.

Prairie Wetlands

More than 10,000 years ago, as the Wisconsin glacier retreated from central North America, it left behind large ice blocks buried in the glacial till. As the ice melted, shallow water-filled depressions were formed. Today we know these millions of small depressions by a variety of names, including prairie potholes, marshes, or sloughs (Voldseth 2004). The region covered by these depressions is referred to as the Prairie Pothole Region (PPR) and covers approximately 777,000 km^2, including portions of Manitoba, Saskatchewan, Alberta, North and South Dakota, Iowa, Minnesota, and Montana (Luoma 1985) (Fig. 1). In Canada, the PPR occupies an area of about 390,000 km^2 or about 5% of the country (National Wetlands Working Group 1988) and covers approximately 80% of western Canada (Batt *et al.* 1989). Although the retreat of the glaciers contributed to the formation of millions of small pothole wetlands across the prairies, the glacial lakes that also formed

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Fig. 1. Map showing the extent of the Prairie Pothole Region in Canada and the United States.

during the retreat contributed to the formation of several large lacustrine or coastal wetlands such as Delta Marsh and Netley-Libau Marsh, present on the southern shores of Lake Manitoba and Lake Winnipeg, respectively (Fig. 2). These small and large wetlands represent important wetland habitat in the prairie region.

Regardless of size, wetlands across the PPR vary greatly in their water chemistry, in their ability to maintain long-term surface water, and in the varieties of aquatic vegetation and fauna they sustain. They exist in a wide range of hydrological settings, where annual and seasonal precipitation varies greatly in both amount and form. Wetlands in Canada are defined as lands that are saturated long enough to promote wetland or aquatic processes, as indicated by poorly drained soils, hydrophytic vegetation, and various kinds of biological activity that are adapted to surviving in wet environments (National Wetlands Working Group 1988). The Canadian Wetland Classification System recognizes five wetland classes, 49 wetland forms and 72 subforms, and eight wetland types (Adams *et al.* 1987, 1997). The five classes include bogs, fens, swamps, shallow water, and marshes. Almost all prairie wetlands belong to the marsh class under this system.

The most in-depth classification system for those interested in both the biology and ecology of wetlands in the PPR is the Stewart and Kantrud (1971) classification system, which was designed for northern prairie wetlands in the Great Plains region of the United States. This system is based on the premise that wetland vegetation can be grouped into zones, each characterized by a different community structure and a distinct assemblage of

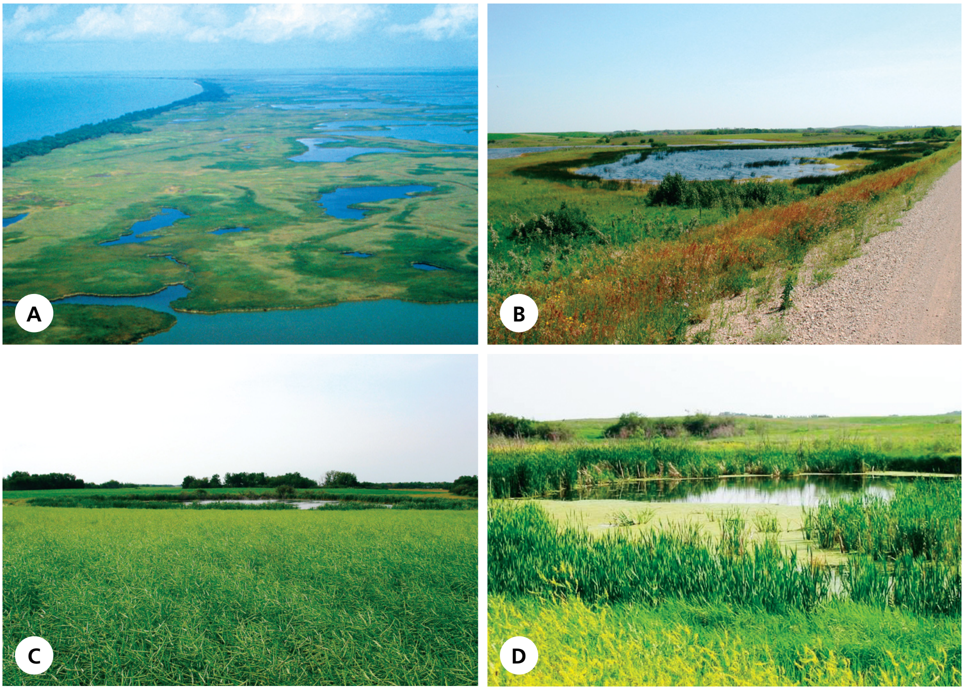

Fig. 2. Examples of wetlands in the Prairie Pothole Region of western Canada. A, Delta Marsh, Manitoba. B, Semi-permanent (Class 4) wetland in central Saskatchewan surrounded by native grasslands. C, Semi-permanent wetland in central Manitoba surrounded by cropland. D, Semi-permanent wetland in Manitoba.

plant species. Zones are closely related to variations in water permanence, modified by the permeability of bottom soils and the influence of groundwater (Stewart and Kantrud 1971). This system recognizes and accounts for seasonal and annual changes in vegetation zones, depending on fluctuations in water level and surrounding land use, such as agriculture.

Wetlands in the PPR are considered both economically and ecologically significant (van der Valk and Pederson 2003). Important ecological functions of wetlands include the storage and release of surface water, recharge of local and regional groundwater supplies, reduction in peak flood-water flows, desynchronization of flood peaks and erosion, and sedimentation prevention (Gabor *et al.* 2004). Prairie wetlands also provide essential habitat for numerous species. Nearly 350 species of plants are found in the wetlands of the southern PPR (Galatowitsch and van der Valk 1998). Wetlands of the PPR are considered the most productive waterfowl habitat in the world and the most important breeding area for waterfowl in North America (Batt *et al.* 1989; Sorenson *et al.* 1998). The value of wetlands to Canadians, if one combines both the ecological and recreational values they provide, is estimated at $20 billion annually (Campbell and Rubec 2003).

The abundant plant and animal diversity of prairie wetlands derives from the fact that they are neither fully aquatic nor fully terrestrial systems. As a result, they often possess characteristics of both. Most prairie wetlands fluctuate, or cycle, from extended flooded conditions during periods of high precipitation to no standing water during drought conditions (van der Valk and Davis 1978; van der Valk 2005). The speed and the extent to which they cycle through this wet/dry hydroperiod ultimately determines the types of

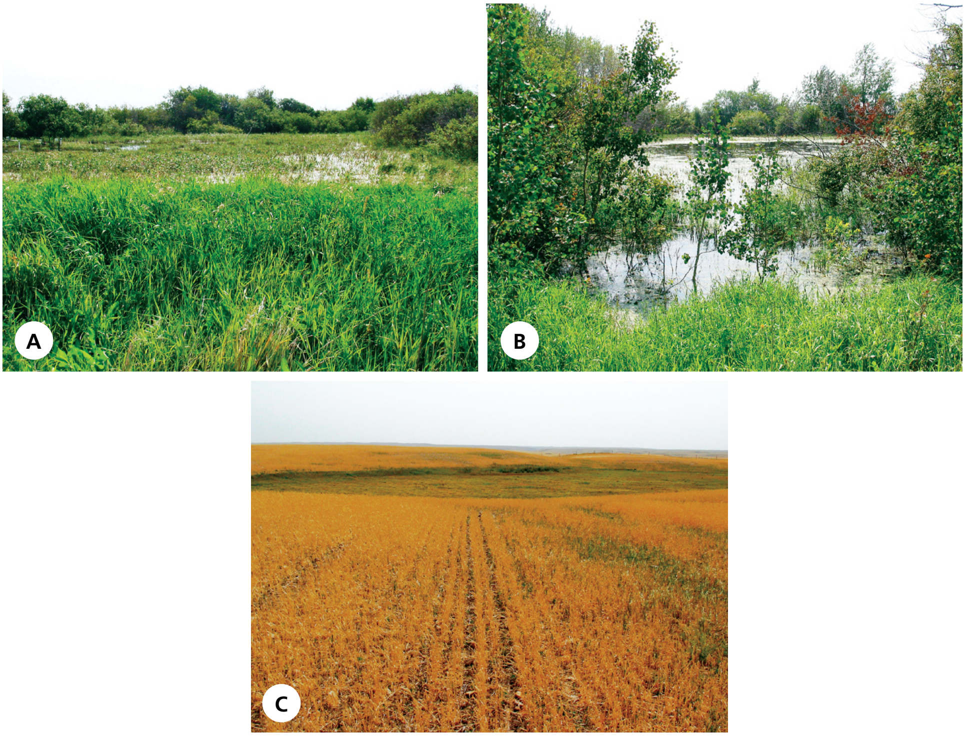

Fig. 3. Examples of seasonal (Class 3) wetlands. A and B, The parkland region. C, The southwestern region of Saskatchewan. All wetlands in these photos are surrounded by croplands.

aquatic and terrestrial plants that occur and their associated biota. In the prairies, most temporary and seasonal wetlands cycle through the wet/dry hydroperiod annually (Fig. 3). Winter snowmelt and spring rains fill these shallow wetlands each spring, and summer evaporation from surface waters and transpiration from plants cause these basins to go dry by mid- to late summer in most years. Wet meadow and shallow marsh vegetation such as fowl bluegrass (*Poa palustris* L.) and wheat sedge (*Carex atherodes* Spreng.) dominate in wetlands flooded for short periods. These plants possess adaptations that allow them to survive the annual wet/dry cycle. In comparison to seasonal and temporary wetlands, semi-permanent and permanent prairie wetlands frequently hold water for many years before they experience a period of drought. Although wet meadow and shallow marsh vegetation still occur around the outer extent of these basins, more flood-tolerant plant species such as hardstem bulrush (*Schoenoplectus acutus* (Muhl. ex Bigelow) A. & D. Löve) and broadleaf cattail (*Typha latifolia* L.) dominate in the deeper flooded areas.

The aquatic biotic communities in prairie wetlands are therefore continually changing as a result of naturally occurring short- and long-term fluctuations in water levels, changes in vegetation, changes in water chemistry, and anthropogenic disturbance (Euliss *et al.* 1999). Anthropogenic disturbances in the prairies include wetland drainage, elevated sedimentation rates, drift of agricultural chemicals, and alteration of surface water flow. All of these disturbances ultimately affect vegetative growth, which, in turn, impacts the associated fauna.

Current Status of Prairie Wetlands

Global estimates of wetland area range from 5.3 to 12.8 million km^2 (Zedler and Kercher 2005). Despite the likelihood that remaining wetlands occupy less than 9% of the Earth's land area, they contribute more to renewable ecosystem services than their small area implies (Zedler and Kercher 2005). Canada has an estimated 127 million ha of wetlands or approximately one-quarter of the world's wetland area (Environment Canada 1991). Although the lack of a national wetland inventory program makes it difficult to estimate wetland loss since the time of settlement (Watmough and Schmoll 2007), it is estimated that 20 million ha have been lost since the 1800s (Environment Canada 1991).

Most wetlands in the PPR exist in agricultural landscapes that are in private ownership (Rickerl *et al.* 2000). There are more than 128 million acres of land in the PPR that are under crop production (Leitch and Fridgen 1998), and agricultural activities affect nearly every wetland directly or indirectly (Kantrud *et al.* 1989). Many landowners view wetlands as non-productive acreage or operational nuisances. Recent work by Watmough and Schmoll (2007) indicates that wetlands continue to be lost and degraded in all ecoregions of the PPR, with certain areas more at risk to wetland loss than other areas (Rakowski *et al.* 1974). Habitat monitoring across the entire PPR showed a 5% reduction in the number of wetland basins from 1985 to 2001 (Watmough and Schmoll 2007). Wetland area during that same period decreased by 6–7%, with the smallest wetlands (mean size = 0.2 ha) at greatest risk of drainage or degradation. Natural upland habitats are also at risk in the PPR. From 1985 to 2001, natural grassland habitats decreased 10%, whereas tame pasture or tame hay areas increased by 113% and 86%, respectively (Watmough and Schmoll 2007). Much of these increases were due to the conversion of annual cropland to tame plantings. What is evident from the Watmough and Schmoll (2007) study is that wetlands in the PPR continue to disappear at a slow but continuing rate (see Fig. 4).

Aquatic Invertebrates of Prairie Wetlands

Wetlands are generally regarded as areas of high productivity and important biodiversity, supporting many species of plants and animals (Gopal *et al.* 2000; Keddy 2000). Wetlands of the PPR are no different, supporting a diversity of aquatic plants, mammals, amphibians, birds, and aquatic invertebrates adapted to these dynamic but productive environments (van der Valk 1989). Prairie potholes have always been regarded as an important habitat for waterfowl. It has been estimated that 50–80% of North American waterfowl breed in the PPR (Batt *et al.* 1989). Consequently, much of the research and conservation activities in prairie wetlands have been directed at understanding the importance of these habitats to waterfowl. More recent research has focused on the importance of prairie wetlands for providing ecological goods and services, such as water storage, water quality preservation, and carbon storage (e.g., Murkin 1998; Gabor *et al.* 2004; Euliss *et al.* 2006; Gleason *et al.* 2008).

Although the prairie wetlands are widely known as an important waterfowl breeding habitat, it was not until the 1960s and 1970s that researchers began to focus on the food habits of breeding and juvenile waterfowl on the prairies. Prior to this time, much of what was known about waterfowl food habits had been gained from waterfowl shot during the fall hunting season (Swanson *et al.* 1979; Krapu and Reinecke 1992). The methods used also biased information about food habits in favour of seeds and other hard plant materials. Little was known about the food habits of waterfowl at other times of the year. This changed, however, with important work done on the breeding grounds (e.g., Perret 1962;

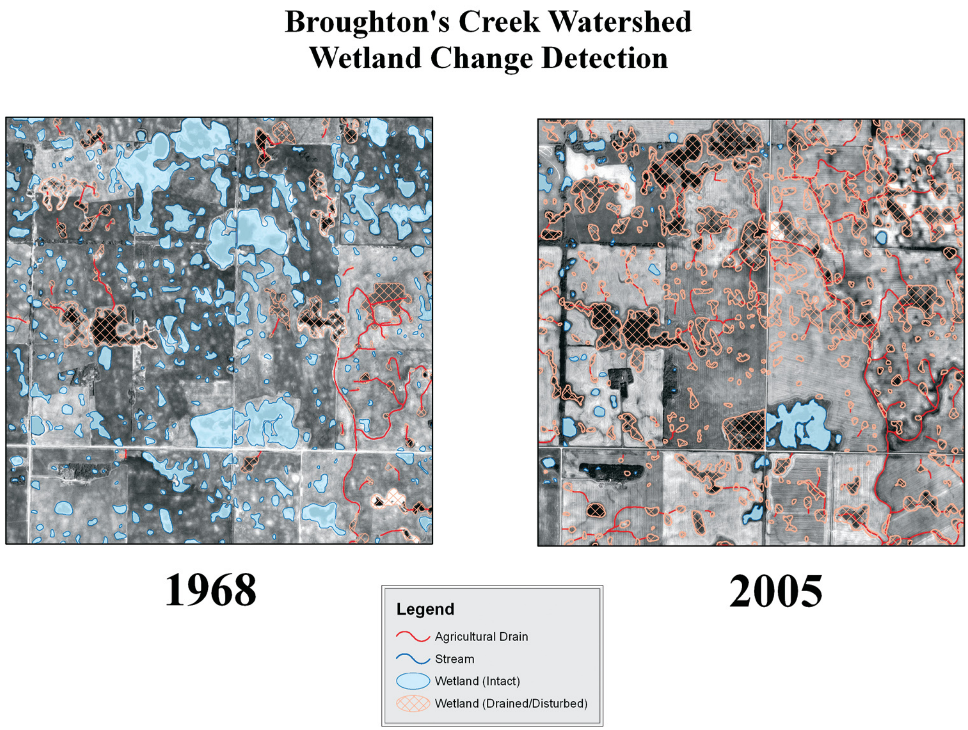

Fig. 4. Example of landscape change and wetland loss from 1968 to 2005 in the Broughton's Creek Watershed in western Manitoba.

Dirschl 1969; Bartonek and Hickey 1969; Swanson and Bartonek 1970; Bartonek 1972; Sugden 1973; Krapu 1974*a*, 1974*b*). These studies, and many that followed, documented the importance of aquatic invertebrates to waterfowl food habits, and this information began to generate interest in the aquatic invertebrate communities of prairie wetlands (Murkin and Batt 1987).

The purpose of this chapter is to provide a general description of the aquatic invertebrate community found in prairie wetland habitats. Emphasis is on the composition of the invertebrate community, important roles within these ecosystems, and how agricultural activities within and around prairie wetlands impact the invertebrate community. Further information on the ecology of aquatic invertebrates, such as their responses to the wet/dry cycle and adaptations to these dynamic habitats, can be found in reviews provided by Euliss *et al.* (1999) and by Murkin and Ross (1999, 2000).

Invertebrate Community Composition

Many studies of prairie wetland invertebrates were done to gain some understanding of the food resources available to waterfowl. Unfortunately, a great deal of that invertebrate work was done without much taxonomic resolution. Identifications were done at higher taxonomic levels, such as class or subclass for non-insects, and order or family for insects. In addition, researchers who studied waterfowl food habits and their associated habitat sampling were primarily interested in those invertebrates consumed by waterfowl. These mostly larger invertebrates, commonly referred to as "macroinvertebrates" were retained by a U.S. Standard No. 35 sieve (0.5-mm mesh) used to wash and clean samples prior to sorting and identification. Methodological difficulties (e.g., small size, specialized techniques, lack of keys) also hindered more thorough identifications (Danks and Rosenberg 1987).

As a consequence of these deficiencies, relatively few species lists for the aquatic invertebrates of prairie wetlands are available. Those that have been assembled are site specific and/or taxonomically restricted (e.g., Driver 1977; Parker 1985, 1992; Hanson and Swanson 1989; Wrubleski and Rosenberg 1990; Wrubleski 1996; Hann 1999; Alperyn 2004; Scudder *et al.* 2010). In addition to these broader community inventories, some detailed ecological studies have looked at a few key species (e.g., Sawchyn and Gillott 1974*a*, 1974*b*, 1975; Rasmussen 1984; Wen 1992; Ross and Murkin 1993), but these studies are also relatively few in number.

Euliss *et al.* (1999) provide the most complete list of aquatic invertebrate species present in prairie pothole wetlands. They listed 323 named species from 23 published sources. In the intervening 10 years, relatively few additional species inventories or lists have been published. Exceptions include Hann and Zrum (1997), Hann (1999), Alperyn (2004), and Scudder *et al.* (2010). Adding the species reported in these papers to those compiled by Euliss *et al.* (1999) results in a total of 401 species of aquatic invertebrates having been identified in the wetlands of the PPR (Table 1). Unnamed or unidentified species are not included in these totals, and so actual numbers of invertebrate species are likely much higher.

Because of the sampling and identification problems noted earlier, it is difficult to compare the numbers of aquatic invertebrate species present in PPR wetlands with other aquatic habitats. However, the diversity of the invertebrate community in wetland habitats is generally reported to be lower than in other larger, more permanent aquatic habitats (Euliss *et al.* 1999; Sharitz and Batzer 1999). For example, there are 68 named species of Chironomidae (Diptera, midges) reported from PPR wetlands (Table 1). This compares to 84 species collected in three fens in northwestern Ontario (Rosenberg *et al.* 1988) and 158 species identified from the littoral zone of a Manitoba boreal lake (Rosenberg *et al.* 1984).

Aquatic invertebrates in prairie wetlands are ecological generalists, also being found in other nearby ecoregions and habitats (Euliss *et al.* 1999; Alperyn 2004; Scudder *et al.* 2010) (Fig. 5). Few species are believed to be confined to only prairie wetlands. This is likely due in part to the harsh conditions found in shallow aquatic systems in northern latitudes. Consequently, prairie wetland invertebrate communities consist primarily of ecological generalists that possess the necessary adaptations to tolerate environmental extremes and can be found in a variety of aquatic habitats (Euliss *et al.* 1999; Alperyn 2004; Scudder *et al.* 2010).

From the studies that have been done, one of the most abundant and diverse groups in PPR wetlands are the Chironomidae. Bataille and Baldassarre (1993), in their study of three prairie potholes near Minnedosa, Manitoba, reported that chironomids represented 71–78% of the total number of emerging insects. Parker (1992) reported that chironomids represented 66–71% of emerging insects from a prairie pond near Saskatoon, Saskatchewan. In prairie pothole habitats of North Dakota, chironomids represented 60% of the insects flying over these habitats and accounted for 32.9% of the total biomass (King and Wrubleski 1998). Parker (1985) reported 36 species of midges from a single semi-permanent prairie pond near Floral, Saskatchewan. Driver (1977) found 48 species in 16 ponds near the same location. Of 115 species of insects emerging from a wetland near Saskatoon, Saskatchewan,

Table 1. Numbers of named aquatic invertebrate taxa reported from wetlands of the Prairie Pothole Region. Species numbers are derived from reports in the indicated references.

Phyla Family	Reported Number of Species	Reference
Gastropoda		
Hydrobiidae	2	2
Lymnaeidae	6	2, 3
Physidae	5	2
Planorbidae	10	2, 3
Valvatidae	1	2
Annelida		
Glossiphoniidae	5	2, 3
Erpobdellidae	2	2
Lumbriculidae	1	2
Naididae	2	2, 3
Tubificidae	1	2
Arthropoda		
Crustacea		
Gammaridae	1	2
Talitridae	1	2
Artemiidae	1	2
Branchinectidae	1	2
Chirocephalidae	2	2
Cyzicidae	1	3
Lynceidae	2	2
Bosminidae	1	2
Chydoridae	13	3
Daphnidae	8	2, 3
Leptodoridae	1	3
Macrothricidae	1	3
Polyphemidae	1	3
Sididae	3	3
Diaptomidae	4	2, 3
Temoridae	1	3
Laophontidae	1	3
Cyprididae	1	2
Insecta		
Baetidae	1	2
Caenidae	1	2
Aeshnidae	5	2
Agrionidae	2	2

Table 1. (continued)

Phyla Family	Reported Number of Species	Reference
Coenagrionidae	15	2
Corduliidae	1	2
Gomphidae	3	2
Lestidae	6	2
Libellulidae	17	2
Dytiscidae	70	1, 2
Gyrinidae	2	2
Haliplidae	6	2
Hydrophilidae	11	2
Belostomatidae	3	2
Corixidae	40	2, 4
Gerridae	7	2
Hydrometridae	1	2
Mesoveliidae	1	2
Nepidae	2	2
Notonectidae	10	2, 4
Pleidae	1	2
Saldidae	9	2
Veliidae	2	2
Sisyridae	1	2
Pyralidae	1	3
Hydroptilidae	1	2
Leptoceridae	2	2
Limnephilidae	6	2
Molannidae	1	2
Phryganeidae	2	2
Polycentropodidae	1	2
Psychomyiidae	1	2
Ceratopogonidae	6	2
Chaoboridae	1	2
Chironomidae	68	2
Culicidae	11	2, 3
Dixidae	1	2
Stratiomyidae	1	2
Tipulidae	1	2
Pteromalidae	1	2
Total	401	

[1] Alperyn (2004); [2] Euliss *et al.* (1999); [3] Hann (1999); [4] Scudder *et al.* (2010).

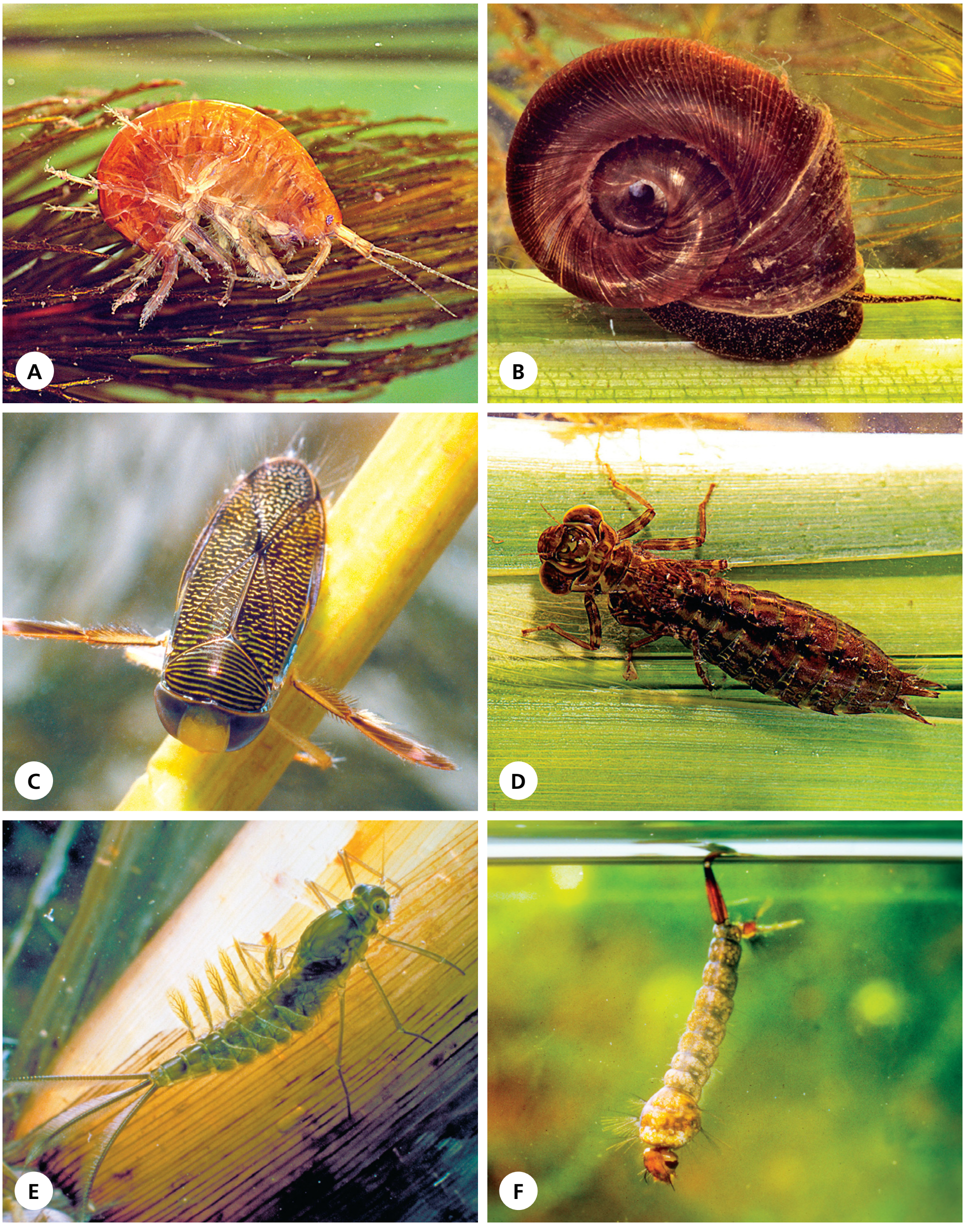

Fig. 5. Common wetland invertebrates. A, Amphipod. B, Pond snail. C, Water boatman. D, Dragonfly nymph. E, Mayfly nymph. F, Mosquito larva.

Parker (1992) reported that 37% (43) of them were midges. Wrubleski and Rosenberg (1990) found 84 species (including unidentified and unnamed species) of midges in a small pond within the larger Delta Marsh.

Another abundant and diverse group in PPR wetlands are the Dytiscidae. Seventy species are listed as occurring in PPR wetlands (Table 1). In prairie potholes of central North

Dakota, Hanson and Swanson (1989) found that 38 of 57 beetle species were Dytiscidae and that they accounted for 76% of all beetles collected.

Probably the best known aquatic invertebrate community in a Canadian prairie wetland is the Delta Marsh on the south shore of Lake Manitoba. This large wetland has the advantage of having two research stations, the Delta Marsh Field Station (University of Manitoba) and the Delta Waterfowl and Wetlands Research Station, which have supported numerous studies of the marsh invertebrate community. One especially important contribution was that of the Marsh Ecology Research Program, which generated 24 publications that have in various ways added to our knowledge of aquatic invertebrates in prairie wetlands (Murkin *et al.* 2000).

Important Functions and Roles of Aquatic Invertebrates in Prairie Wetlands

The most well-known function of aquatic invertebrates in prairie wetland habitats is as a food resource for waterfowl and other wetland fauna. During waterfowl nesting and brood rearing, aquatic invertebrates make up a significant portion of waterfowl foods (see reviews by Murkin and Batt 1987; Swanson and Duebbert 1989; Krapu and Reinecke 1992; Sedinger 1992). Invertebrates provide an important source of protein and several essential amino acids for gonadal development and egg laying. They are also a rich source of lipids and energy (Driver *et al.* 1974; Afton and Ankney 1991). Gastropods and crustaceans are an important source of calcium needed for eggshell formation during laying (Krapu and Reinecke 1992).

Invertebrates are so important to waterfowl that they can influence spring habitat selection (Joyner 1980; Talent *et al.* 1982; Murkin and Kadlec 1986; Hanson and Butler 1994). Lesser Scaup (*Aythya affinis* (Eyton)) preferentially forage in wetlands with high amphipod (*Gammarus lacustris* G.O. Sars, *Hyalella azteca* Saussure) densities, especially during spring migration (Lindeman and Clark 1999; Anteau and Afton 2006, 2009). The continental decline in Lesser Scaup populations has been suggested to be due in part to declining numbers of wetlands supporting amphipod populations (Anteau and Afton 2008, 2009). The availability of wetland invertebrates can also affect duckling growth rates and survival (Cox *et al.* 1998; Sjöberg *et al.* 2000).

Aquatic invertebrates are also important food resources for other prairie wetland fauna. Wetland passerines such as Red-winged Blackbirds (*Agelaius phoeniceus* L.) and Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus* (Bonaparte)) rely on aquatic insects (Voigts 1973; Wilson 1978), as do many shorebirds, grebes, and other wetland birds (Murkin and Batt 1987; Euliss *et al.* 1999). Adult aquatic insects originating from wetland habitats provide an important food resource for many non-wetland birds (e.g., Sealy 1980; Guinan and Sealy 1987). Wetland fish, both native and stocked, and amphibians also rely heavily on aquatic invertebrates (Held and Peterka 1974; Olenick and Gee 1981; Duffy 1998; Benoy *et al.* 2002).

High rates of primary productivity by the emergent macrophyte communities in prairie wetlands result in the production of abundant detrital material. Much of this accumulated energy and nutrients was believed to be passed on to higher trophic levels through decomposition and the action of aquatic invertebrate detritivores (Murkin 1989). However, the role that aquatic invertebrates play in the consumption and breakdown of plant litter in prairie wetlands is not clear. Macrophyte litter and the associated microbial community have generally been assumed to be important food resources of wetland invertebrates. However, relatively little evidence is available to support this assumption. For example, Bicknese

(1987) found that invertebrates had little influence on litter decomposition dynamics in a prairie marsh.

There are few published reports on the food habits of invertebrates in these habitats (Murkin 1989). Rasmussen (1984) reported that the larvae of two chironomid species relied heavily on algae and algal detritus as their principal food resource in a prairie pond near Calgary, Alberta. Algae are also known to be an important food resource for many other aquatic invertebrates (reviewed in Lamberti and Moore 1984; Lamberti 1996) that occur in wetland habitats. Experimental manipulations of algal abundances have shown equivocal responses by aquatic invertebrates. Murkin *et al.* (1991) observed higher invertebrate abundances in a wetland receiving nutrient inputs through agricultural runoff compared with nutrient-poor wetlands in the same area. In mesocosm studies, Campeau *et al.* (1994), Gabor *et al.* (1994), and Hann and Goldsborough (1997) demonstrated increased invertebrate abundance in response to fertilizer additions and increased algal biomass. However, Murkin *et al.* (1994) observed no responses by aquatic invertebrates to similar experimental manipulations.

Stable isotope measurements of carbon, nitrogen, and sulphur are useful in determining food-web structure in aquatic and terrestrial systems, including wetlands (see Peterson and Fry 1987; Rundel *et al.* 1989; Lajtha and Michener 1994). Keough *et al.* (1996) identified phytoplankton as an important food-web component in a Lake Superior coastal wetland. Neill and Cornwell (1992) were unable to show conclusive matching of stable isotope signatures, but suggested that an unidentified algal community may be important in supporting food webs in prairie marshes. This suggestion was subsequently confirmed by Euliss *et al.* (1999), who reported that in prairie pothole wetlands, algae (phytoplankton and periphyton) are important food resources for aquatic invertebrates.

Given that aquatic invertebrates rely on macrophytes and algae as food resources, invertebrates can, in turn, impact the distribution and abundance of these food resources. For example, invertebrate grazing has been found to be important in structuring wetland algal communities and regulating algal productivity (Hann 1991; Hann and Goldsborough 1997). Zimmer *et al.* (2003) found that the presence of fathead minnows resulted in reductions in cladocerans, which, in turn, resulted in reduced grazing pressure, higher phytoplankton levels, and increased turbidity of the water column. Gastropod grazing can influence the distribution, abundance, and diversity of submersed macrophytes (Sheldon 1987). Terrestrial insects can be important grazers of emergent macrophytes in wetlands (e.g., Penko and Pratt 1986, 1987; Foote *et al.* 1988), but this has not been well-documented in prairie wetlands.

Agricultural Effects on Prairie Wetlands and Aquatic Invertebrates

Most wetlands in the PPR are embedded within agricultural landscapes, where they are subject to varying degrees of disturbance from activities such as drainage, consolidation, grazing, cultivation, filling, or burning (Gleason and Euliss 1998; Bartzen *et al.* 2010) (Fig. 6). In Canada, it is estimated that 85% of wetland loss is due to agricultural activities or urban development (Wiken *et al.* 2003). Estimates of wetland loss or degradation in the PPR from agriculture are 1.2 million ha (Glooschenko *et al.* 1993). A Canadian study of 10,000 prairie wetlands found that 79% of wetland margins had been degraded by agriculture (Turner *et al.* 1987). In addition to the physical destruction of the wetland edge by cultivation, soil compaction, and vegetation removal, other effects include large inputs of sediments, fertilizers, and other agricultural chemicals (Neely and Baker

Fig. 6. Examples of agricultural impacts on wetlands. A, Wetland drainage and consolidation. B, Grazing and livestock watering. C, Cultivation. D, Cultivation of the riparian edge.

1989; Goldsborough and Crumpton 1998). Although most studies have focused on the consequences of anthropogenic stress from severe disruptions such as wetland drainage or consolidation, many land-use impacts, such as the ongoing deterioration of the marsh edge, tend to be less severe (Schindler 1987). The risk in not understanding or examining both severe and less severe impacts on wetlands within agricultural landscapes is not being able to predict future outcomes or long-term effects on wetland communities such as the aquatic invertebrates.

Grazing

The intensive livestock industry is anticipated to grow in many regions of Canada, with meat and meat products representing the largest single subsector of agricultural exports (Agriculture and Agri-Food Canada 1998; Harker *et al.* 2004). As a result, the demand on Canada's grassland resources may exceed the ability of the landscape to sustain itself. For example, intense livestock grazing can lead to increased overland surface flow from factors such as soil compaction, decreases in soil organic matter content, infiltrability, and soil water-holding capacity. These factors have been shown to lead to the stabilization of wetland water levels because of increased runoff, particularly during spring snowmelt (Gifford and Hawkins 1978; Euliss and Mushet 1996). Casey *et al.* (1999) studied the effect of grazing intensity on aquatic invertebrates in wetlands located in central Alberta. Macroinvertebrate densities were found to be lower in wetlands within grasslands conventionally grazed compared with wetlands in deferred (grazing delayed until July 15th) or ungrazed grasslands. Certain invertebrate species such as Chironomidae dominated wetlands in ungrazed grasslands, whereas *Hyalella azteca* was found almost exclusively in those wetlands in conventionally grazed grasslands. *Hyalella's* presence within a wetland can be a good indication that the hydrology of a wetland has remained stable for many years (Murkin and Ross 1999). Therefore, the presence of *H. azteca* in wetlands within continuously grazed grasslands could be the result of a much more stable hydrology for wetlands located in heavily grazed landscapes.

Evidence also suggests that grazing intensity can affect the amount of nutrients lost from upland grassland landscapes and transferred into low-lying wetlands. Receiving waters vary in their sensitivity to these excess nutrients and sediments (Clark 1998). Impacts on lentic systems, such as wetlands, may be greater because pollutants and sediments tend to accumulate. Flowing water systems, such as streams, may be affected less because of their ability to self-flush or clean (Clark 1998). Scrimgeour and Kendall (2003) report on the impact of livestock grazing on stream benthic invertebrates in the Cypress Hills grassland plateau near Medicine Hat, Alberta. No differences in species diversity were found between heavily grazed and ungrazed watersheds. However, the aquatic invertebrate biomass increased in streams located within grazed watersheds. This was due to specific biomass increases of large oligochaetes, leeches, dytiscid beetles, and physid gastropods in downstream locations. Oligochaetes, gastropods, and leeches are often used as indicators of poor water quality (Pratt *et al.* 1981; Resh and Rosenberg 1984; Gray 2004).

Hornung and Rice (2003) examined the aquatic invertebrate community, water chemistry, and vegetation of wetlands within grazed and ungrazed landscapes in southern Alberta. They found a negative correlation between vegetative species richness and the presence of cattle. Orthophosphates and ammonium levels were also consistently higher in wetlands with cattle present. Although they found no significant trends in overall macroinvertebrate species diversity, composition, or abundance between ungrazed, moderately grazed, and heavily grazed sites, odonate diversity did decline significantly as grazing intensity increased. Certain species, such as *Aeshna interrupta* Walker and *Coenagrion angulatum* Walker, were affected by a loss of plant stem density at grazed sites, and other species, such as *Enallagma ebrium* (Hagen), were affected by a loss of vegetation species richness. Overall, odonate species richness demonstrated a significant negative relationship with the mean percentage of stems grazed. The researchers attributed these impacts to the direct influence that grazing has on critical odonate habitat through the modification of submersed, emergent, and surrounding vegetation; the trampling of shoreline microhabitat; and the deterioration of water quality from urination and defecation. The physical destruction of vegetation results in the loss of mating sites, microhabitat and cover for larvae, and emergence locations for nymphs.

Sedimentation

Sedimentation is one of the major water-quality concerns in Canada and the United States. Excessive sediment loading is considered to be the major pollutant of wetlands, rivers, lakes, and estuaries in the United States (Gleason and Euliss 1998; Zimmerman *et al.* 2003). Tillage erosion, soil translocation, and the redistribution of soil nutrients in agricultural fields can be substantial in hummocky landscapes (Arndt and Richardson 1988; Govers *et al.* 1999; Lobb *et al.* 1995; Pennock 2003; Li *et al.* 2007; Smith *et al.* 2008). Agricultural practices and erosive processes move soil from upper-slope locations in fields to lower-slope locations, where wetlands are often situated. Pennock (2005) found that the rate of soil loss at shoulder-slope positions for five cultivated sites in Saskatchewan averaged 33 t ha^{-1} yr^{-1}, with a mean soil gain downslope of 15.2 t ha^{-1} yr^{-1}. Rates of sedimentation in wetlands have been reported to vary from 0.5 cm yr^{-1} to 3–4 cm yr^{-1} (Johnston *et al.* 1984; Fennessey *et al.* 1994). Smith *et al.* (2008) found that the amount of nitrate–nitrogen (NO_3–N) in the top 15 cm of soil at convex upper-slope positions was doubled when accumulated topsoil from lower slope areas was moved back to the hilltop locations. This finding suggests that nutrients in the soil, such as nitrogen and phosphorous, also have the potential to accumulate in wetlands.

One impact of sedimentation on wetland invertebrate communities is the subtle shift it causes in plant communities. Even small amounts of overlying soil can affect seed germination, as well as species richness and diversity (Galinato and van der Valk 1986; Dittmar and Neely 1999; Werner and Zedler 2002). Galinato and van der Valk (1986) found that wetland/riparian plant seed germination decreased from 79% to 38% for annuals and from 71% to 20% for perennials when covered by 1 cm of soil. Only *Hordeum jubatum* L., an invasive perennial, was able to establish successfully under all soil depths tested. Mahaney *et al.* (2004) found that all plant seeds collected from pristine wetlands in Pennsylvania were affected by 1 cm of overlying sediments, whereas invasive species collected from wetlands, such as *Phalaris arundinacea* L. and *Cirsium arvense* (L.) Scop., were not. Plants belonging to the *Carex* genus, more than almost all other genera, display a marked requirement for light in order to germinate (Schutz and Rave 1999). This requirement is a concern because *Carex* species are an essential plant community in prairie wetlands, with more than 60 species listed in the PPR (Barkley 1986). Most seeds have difficulty germinating in environmental conditions that are low in both oxygen and light (Bewley and Black 1994; Baskin and Baskin 1998), resulting in the buried seeds of many plants remaining dormant (Fenner 1987). For wetland and riparian plants with small seeds, the combination of low light and oxygen can make germination even more difficult (Galinato and van der Valk 1986).

Gleason *et al.* (2003) state that the cultivation of dry wetlands, in conjunction with sediment inputs, may severely impact the recovery of invertebrate populations during wet periods. Cultivation may also decrease the survivorship and fecundity of existing invertebrate populations in wetlands that dry frequently (Arruda *et al.* 1983; Kirk and Gilbert 1990). Part of the reason for this relates to the detrimental effect that excess sediments have on primary production in prairie wetlands and on the food chain (Gleason and Euliss 1998). The most severe impact occurs when wetlands fill with so much sediment that they no longer hold water (Gleason and Euliss 1998). Using sediment samples collected from seasonal and semi-permanent wetlands in North Dakota, Gleason *et al.* (2003) found that only 0.5 cm of additional sediment was required to eliminate emergence of nearly all aquatic invertebrates from the soil egg bank. Ostracods, cladocerans, and copepods were the only taxa to successfully incubate in their experiments. These researchers found that 2 cm of sediment led to a 92% failure rate in hatching. They also found that 0.5 cm of sediments virtually halted all plant seedling emergence.

Wetland Drainage and Consolidation

Many wetlands in the PPR are drained or consolidated into larger wetlands to increase crop production and to eliminate the nuisance of manoeuvring large farm equipment around them in the field (Hubbard and Linder 1986). Besides the partial or complete destruction of a wetland's hydrology, drainage has also been implicated as a cause for decreased water tables and increased flood frequencies in certain locations (Rannie 1980; Miller and Nudds 1996).

Many wetland invertebrates have developed specific physiological features that allow them to survive when wetlands go dry. Cladocerans, ostracods, copepods, and certain gastropods are common wetland invertebrates that are able to withstand drought conditions (Murkin and Ross 1999). Numerous other invertebrates, such as amphipods, are not capable of surviving dry periods and will die when wetlands go dry. Those insects capable of flight, such as flies, beetles, bugs, and odonates, will disperse to more favourable locations during dry periods. When the water returns, either in the form of snowmelt or summer rains, wetland invertebrates with drought-resistant stages or those capable of flight will be the first to appear. The remaining invertebrates will be able to repopulate a wetland only through passive means, such as through adjoining waterways or by being carried in the feathers or fur of water birds and mammals (e.g., Daborn 1976; Swanson 1984; Boag 1986).

There is no doubt that the most destructive event a prairie wetland can be subjected to is complete drainage. Unfortunately, drainage has long been recognized as an integral part of agricultural activity throughout the world, especially in western Canada. Drainage has resulted in a dramatic loss of wetland area and wetland function (Walters and Shrubsole 2003). Wetland invertebrates are designed not only to survive, but thrive, with water-level fluctuations in wetlands. Although these normal fluctuations are often short lived, active wetland drainage can result in years or even decades of drought conditions. Drought conditions of this magnitude result in the total destruction of the aquatic invertebrate community. Few wetland invertebrates are capable of withstanding multiple or extended periods of drought (Murkin and Ross 2000) and only a very few, such as fairy shrimp, can withstand dry periods lasting many years in a row. Drainage affects not only the invertebrate community, but the plant community as well (Galatowitsch and van der Valk 1998). Few plant seeds, except those belonging to species such as cattail (*Typha* spp.), are able to germinate after multiple years of drought (Galatowitsch and van der Valk 1998). Wet meadow and low prairie plant seeds are particularly susceptible to degradation after extended periods of drying conditions. Therefore, even when water is restored to drained wetlands, those critical links that once existed between invertebrates and the plant communities will be severely degraded.

Wetland consolidation is the drainage of smaller wetland basins into larger, more permanent wetlands. Many do not view this as an impact because water still remains on the landscape. The loss of these smaller basins, however, leads to a loss in biodiversity of invertebrate and plant species (Ross 2009), as well as to a loss of those invertebrates that thrive on the more frequent wet/dry periods that exist in temporary and seasonal wetlands (Murkin and Ross 1999, 2000). Many of these small wetland basins also provide critical habitat for prairie wildlife and for water birds, particularly during the spring months (Murkin and Ross 1999). Although larger wetlands also have a critical role for many wildlife and water-bird species, it is the presence of both ephemeral and more permanent wetland habitats on the landscape that provide the greatest benefit.

Pesticides

Farmers annually apply a diversity of herbicides and insecticides to crops, either through ground or aerial application, to maximize yields (Donald *et al.* 1999). Pesticides applied to agricultural land can be lost to groundwater and surface water (Hallberg 1985) and can enter wetlands as runoff from summer rains (Donald *et al.* 2005), as snowmelt in the spring (Wauchope 1978; Nicholaichuk and Grover 1983; Fawcett *et al.* 1994), or through the volatilization of pesticides from regional fields to the atmosphere (Grover *et al.* 1976, 1997; Waite *et al.* 1995). Donald *et al.* (1999) detected nine herbicides and two insecticides in a study of 51 Saskatchewan wetlands, with six being the maximum number of pesticides detected in a single wetland. Friesen-Pankratz (2004) conducted a similar study of wetlands across the PPR region and found 62% of wetlands contaminated with pesticides. Donald *et al.* (1999) modelled potential wetland contamination by using Ducks Unlimited Canada wetland data and Environment Canada precipitation data. In the year of their study, they estimated that 9% of Saskatchewan wetlands were exposed to pesticide levels that exceeded guideline limits. A further look at precipitation patterns for Saskatchewan across a number of years revealed that, in any given year, between 2% and 24% of Saskatchewan wetlands could be exposed to pesticide levels that exceed guidelines for the protection of aquatic life.

Although most herbicides exert their toxic effect by impeding photosynthesis, pesticides are designed to kill pests through interference with essential life processes by affecting normal neurological functions (Friesen-Pankratz 2004). Aquatic invertebrates can be exposed by eating contaminated food, by absorbing the pesticide through the gills or skin, by drinking contaminated water, by breathing the pesticide, or by swallowing the pesticide while grooming (Hamilton 1993). The worst effects of pesticides are those that alter predator avoidance (i.e., swimming patterns), reproduction (i.e., a reduction in reproduction rates), or how invertebrates compete for living space and food (Hamilton 1993). Dramatic impacts can ultimately lead to an altered community or habitat structure (Forsyth *et al.* 1997).

Changes to plant habitat structure can occur in two ways: through contact herbicides or through translocated herbicides. Contact herbicides affect only the plant parts that they actually come into contact with, whereas translocated herbicides move to other parts of the plant from the point of application (Hamilton 1993). Forsyth *et al.* (1997) found that the potential impact on wetland macrophytes was significant when these plants were exposed to the herbicide clopyralid and to a lesser extent picloram. Their results indicate that 2,4-D dimethylamine salt introduced to prairie ponds at 0.1 mg L^{-1} could eliminate both watermilfoil (*Myriophyllum sibiricum* Komarov) and sago pondweed (*Stuckenia pectinata* (L.) Börner) by the end of one growing season. Habitat losses such as these have the potential to drastically reduce those nektonic invertebrate populations that depend on submersed plant communities while favouring the establishment of benthic invertebrates (Hurlbert 1975; Newbold 1975).

Few studies have examined the impact of pesticides on the overall biodiversity and invertebrate abundance in wetland systems. Wayland (1991) studied the effect of carbofuran on macroinvertebrate numbers and biomass within a series of wetland enclosures in Alberta. No detectable effects were observed at the lower concentration level of 5 $\mu g\ L^{-1}$. At concentration levels of 25 $\mu g\ L^{-1}$, the abundance and biomass of *Hyalella azteca* and the biomass of *Chironomus* (Diptera) larvae decreased. Morill and Neal (1990) found that the application of deltamethrin at normal agricultural dosages to two Saskatchewan ponds led to a decrease in chironomid larvae to approximately 1% of their pre-treatment densities.

Although single-species toxicity studies are invaluable for assessing the lethality of various chemicals, studies that examine the effect of pesticides within the natural environment in which taxa live are important for understanding both indirect and direct impacts. Relyea (2005) examined the effect of four globally common pesticides (carbaryl, malathion, glyphosate, and 2,4-D) on wetland communities containing algae and 25 species of animals. He found the four pesticides to have a profound impact on both the diversity and productivity of the aquatic community, with specific effects depending on the chemical itself. The two insecticides reduced the diversity and biomass of insect predators such as dytiscids (Coleoptera) and notonectids (Hemiptera) and completely eliminated some zooplankton communities such as cladocerans. Tadpole survival and biomass of the wood frog (*Rana sylvatica* LeConte) and the leopard frog (*Lithobates pipiens* (Schreber)), along with spotted salamander (*Ambystoma maculatum* (Shaw)) larvae, increased by 44%, 30%, and 37%, respectively, as insect predators were eliminated. However, these increases were only significant with the addition of carbaryl and not malathion, suggesting that different pesticides may affect the foraging behaviour of the surviving predators differently. The herbicide Roundup reduced tadpole richness by 70% by completely exterminating leopard frogs and gray tree frogs (*Hyla versicolor* LeConte) and nearly exterminating wood frogs. These decreases resulted in a positive effect on the periphyton that the tadpoles consume. 2,4-D, on the other hand, had no effect on the invertebrate community. More studies are needed on the effect that pesticides have on natural wetland systems and whether or not they are contributing to the global decline of biodiversity (Reylea 2005).

Fish

Drainage and consolidation are changing the character of the remaining wetlands in the PPR. Temporary and seasonal wetlands are being drained into larger semi-permanent and permanent wetlands, making them a more permanent fixture on the landscape. Permanent wetlands provide habitat for fish, which historically had much lower abundances in prairie wetlands (Lawler *et al.* 1974; Peterka 1989). In addition, fish are being stocked in PPR wetlands to support the baitfish industry (e.g., fathead minnows (*Pimephales promelas* Rafinesque)) and for human consumption (rainbow trout; *Oncorhynchus mykiss* (Walbaum)) (Olenick and Gee 1981; Hanson and Riggs 1995).

Fish in wetlands, particularly fathead minnows and brook sticklebacks (*Culaea inconstans* (Kirtland)), can exert broad influences on aquatic invertebrate communities by both biotic and abiotic means. Hanson and Riggs (1995) found that indices of aquatic invertebrate abundance, biomass, and taxon richness were all lower in semi-permanent wetlands containing fathead minnows. Zimmer *et al.* (2002) found fathead minnows to be an important determinant of many abiotic and biotic characteristics of wetlands in the eastern PPR of the United States. Wetlands with minnows had fewer aquatic insects overall, with fewer small- and large-bodied cladocerans, ostracods, and copepods. The number of cladocerans and calanoid copepods were, on average, 26 and 19 times higher in fishless wetlands. These researchers also found that wetlands with minnows had a higher abundance of corixids, along with greater turbidity and phytoplankton biomass (chlorophyll *a*). Fishless wetlands also had a more extensive development of submersed macrophytes (Zimmer *et al.* 2003). Although the researchers state that the mechanisms regulating phytoplankton biomass and nutrient concentrations in shallow-water ecosystems are complex, their results suggest that the presence or absence of fish and the abundance and community composition of submersed macrophytes and invertebrates are particularly important in prairie wetlands. Wetlands with fish were found to exhibit characteristics of a turbid-water state, whereas fishless wetlands exemplify the clear-water alternative. This could be due to a reduction of grazing pressure by zooplankton in those wetlands containing fish.

Future Needs

Much research has been done to document the importance of aquatic invertebrates in prairie wetland food webs. However, the other roles and functions of the invertebrates within these habitats are not well-known and interest in the aquatic invertebrates of prairie wetlands has declined. This is likely due in part to a shift by waterfowl researchers away from studies of waterfowl food habits and prairie wetland ecology to increased interest in waterfowl habitat requirements, particularly upland nesting habitat and factors affecting nesting success

(Johnson *et al.* 1987). In addition, the current emphasis on quantifying the ecological goods and services provided by prairie wetlands has shifted the focus away from wetland ecology to the broader role of wetlands in the landscape. Some research continues, mostly related to the use of aquatic invertebrates as bioindicators of anthropogenic effects, particularly agricultural effects on prairie wetlands (e.g., Euliss and Mushet 1999; Euliss *et al.* 2002; Gleason *et al.* 2003) and their role in wetland food webs and water quality (Zimmer *et al.* 2001, 2002, 2003), with much of this work being done in the southern prairie region.

The lack of information on taxonomic composition and basic ecology of prairie wetland aquatic invertebrates restricts our understanding of their importance in the trophic dynamics and functioning of these habitats. More work is needed to identify the members of the invertebrate community, and basic ecological information is needed to fully appreciate their role in these ecosystems. This information would also help us to better understand the factors that regulate community composition and abundance, and how agriculture and other impacts are contributing to losses of wetland biodiversity and function. Add to this the projections for the impacts of climate change on prairie wetlands (e.g., Poiani and Johnson 1993; Johnson *et al.* 2005), and it becomes important for this work to be done soon.

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