Wetlands of the Prairie Pothole Region: Invertebrate Species Composition, Ecology, and Management

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The Prairie Pothole Region (PPR) of the United States and Canada is a unique area where shallow depressions created by the scouring action of Pleistocene glaciation interact with mid-continental climate variations to create and maintain a variety of wetland classes. These wetlands possess unique environmental and biotic characteristics that add to the overall regional diversity and production of aquatic invertebrates and the vertebrate wildlife that depend upon them as food. Climatic extremes in the PPR have a profound and dynamic influence on wetland hydrology, hydroperiod, chemistry, and ultimately the biota. Available knowledge of aquatic invertebrates in the PPR suggests that diversity of invertebrates within each wetland class is low. Harsh environmental conditions range from frigid winter temperatures that freeze wetlands and their sediments to hot summer temperatures and drought conditions that create steep salinity gradients and seasonally dry habitats. Consequently, the invertebrate community is composed mostly of ecological generalists that possess the necessary adaptations to tolerate environmental extremes. In this review, we describe the highly dynamic nature of prairie pothole wetlands and suggest that invertebrate studies be evaluated within a conceptual framework that considers important hydrologic, chemical, and climatic events.

Prairie Pothole Wetlands

The prairie pothole region (PPR) of North America covers approximately 715,000 km^2, extending from north-central Iowa to central Alberta (Figure 21.1). The landscape of the PPR is largely the result of glaciation events during the Pleistocene Epoch. The last glaciers retreated from the PPR approximately 12,000 years ago, leaving behind a landscape dotted with many small depressional wetlands called *potholes* or *sloughs*. The present climate of the midcontinent PPR is dynamic, characterized by interannual variation between wet and dry periods in which abundant rainfall can be followed by drought (i.e., the wet/dry cycle). The association between prairie wetlands and groundwater tables of the region is complex and dynamic. Hydrologically, prairie wetlands can function as groundwater recharge sites, flow-through systems, or groundwater discharge sites. The hydrologic function a particular wetland performs is determined by variations in climate, its position in the landscape, the configuration of the associated water table, and the type of underlying geological substrate. The unique hydrology and climate of this region have a profound influence on the water chemistry, hydroperiod, and ultimately the biotic communities that inhabit prairie wetlands.

Figure 21.1. The prairie pothole region (PPR) of North America.

Aquatic invertebrates inhabiting prairie pothole wetlands are well suited to cope with the highly dynamic and harsh environmental conditions of the PPR. Because of midcontinent temperature and precipitation extremes, wetlands of the PPR periodically go dry, freeze solidly in winter, and exhibit steep salinity gradients. These salinity gradients are due to the interrelation among precipitation, evapotranspiration, interaction with groundwater, and variation in the composition of soils. Due to the harsh environmental conditions of the PPR, the overall diversity of aquatic invertebrates within each wetland is low because taxa are mostly restricted to a few ecological generalists. Those that do occur possess the necessary adaptations that allow them to exploit the naturally high productivity of prairie wetlands.

Despite the harsh climate, the PPR is an extremely productive area for both agricultural products and wildlife. The landscape has been substantially altered since settlement of the PPR in the late 1800s. Economic incentives to convert natural landscapes to agriculture are great and have resulted in the loss of over half of the original 8 million hectares of wetlands (Tiner 1984, Dahl 1990, Dahl and Johnson 1991). Land-use impacts on wetland biota include enhanced siltation rates, contamination from agricultural chemicals, altered hydrology, the spread of exotic plants, and habitat fragmentation due to wetland drainage and conversion of native prairie grasslands into agricultural fields.

The highly dynamic PPR is a unique area that is of critical importance to migratory birds in North America and to the aquatic invertebrates that supply them with dietary nutrients. Despite the value of the knowledge generated thus far, a critical need still exists to expand our knowledge of wetland invertebrates to better our understanding of the PPR ecosystem and its susceptibility to anthropogenic influence. Given the highly dynamic nature of PPR wetlands and the extreme variation in chemical characteristics and hydroperiod, it is essential that invertebrate studies be placed in the proper conceptual framework to maximize the application of study results. Herein we describe the highly dynamic nature of prairie wetlands and suggest that invertebrate studies be evaluated within the context of hydrologic, chemical, and climatic events that characterize the region.

Geology
Glaciation events during the Pleistocene Epoch were the dominant forces that shaped the landscape of the PPR (Winter 1989). When the glaciers retreated, a landscape dotted with numerous small, saucer-like depressions was exposed. These depressions, caused by the uneven deposition of glacial till, the scouring action of glaciers, and the melting of large, buried iceblocks are known today as prairie potholes or sloughs.

The deposition of glacial till was unevenly distributed throughout the PPR. Large moraines accumulated along the terminal ends of glaciers and formed ridges of low, rolling hills in a northwest to southeast orientation, such as the Missouri Coteau. Where glaciers retreated quickly, large, gently rolling areas of glaciated plains were formed, and extremely flat lake beds developed where glaciers dammed meltwater. Due to the geologically young nature of the landscape and moderate rainfall, there are few natural surface drainage systems. Consequently, most wetlands in the PPR are not connected by overland flow.

Climate
The PPR is in the midcontinent of North America and is subject to the climatic extremes of this region (Winter 1989). Temperatures can exceed 40° C in summer and -40° C in winter. Isolated summer thunderstorms may bring several inches of rain in small localized areas while leaving adjacent habitats entirely dry. Also, winds of 50 to 60 km hr^{-1} can quickly dry wetlands during the summer or create windchills below -60° C during winter.

Besides the normal seasonal climatic extremes, the semiarid PPR also undergoes long periods of drought followed by long periods of abundant rainfall. These wet/dry cycles can persist for 10 to 20 years (Duvick and Blasing 1981, Karl and Koscielny 1982, Karl and Riebsame 1984, Diaz 1983, 1986). During periods of severe drought, most wetlands go dry during summer, and many remain completely dry throughout the drought years. Exposure of mud flats upon dewatering is necessary for the germination of many emergent macrophytes, and it facilitates the oxidation of organic sediments and nutrient releases that maintain high productivity. When abundant precipitation returns, wetlands

fill with water and much of the emergent vegetation is drowned. Changes in water permanence and hydroperiod by normal seasonal drawdown and long interannual wet/dry cycles has a profound influence on all PPR biota, but is most easily observed in the hydrophytic community (van der Valk and Davis 1978a).

The PPR has a north-to-south and a west-to-east precipitation gradient, with areas to the north and west receiving less precipitation than those to the south and east. However, even in the wetter southeastern portion of the region, wetlands have a negative water balance. Evaporation exceeds precipitation by 60 cm in southwestern Saskatchewan and eastern Montana and by 10 cm in Iowa (Winter 1989). Despite this negative water balance, many wetlands contain water throughout the year and go dry during periods of extended drought.

Hydrology
Although PPR wetlands receive the majority of their water from snowmelt runoff in the spring and rarely as summer precipitation, the association between prairie wetlands and groundwater tables of the region is complex and dynamic (Winter and Rosenberry 1995). Hydrologically, prairie wetlands can function as groundwater recharge sites, flow-through systems, or groundwater discharge sites. Groundwater recharge wetlands receive their water primarily from the atmosphere and there is little or no groundwater inflow. As a result, the mineral content of water in recharge wetlands is extremely low. Wetlands that function as flow-through systems both receive and discharge water and solutes from and into the ground. Water in flow-through wetlands generally reflects the chemical composition of groundwater. Wetlands that function as groundwater discharge sites receive the bulk of their solutes from groundwater and their principal water loss is from evapotranspiration. As a result, the salinity of water in discharge wetlands can be highly variable and in some cases can exceed the salinity of seawater. The hydrologic function (recharge, discharge, flow-through) of a particular wetland is determined by variations in climate and by their position in the landscape, the configuration of the associated water table, and the type of underlying geologic substrate. The hydrologic function of individual wetlands defines their unique hydroperiod and chemical characteristics and ultimately the plant community they support. Hence, wetland classes based on vegetation (Stewart and Kantrud 1971) reflect the range of hydrologic function within any given wetland class. Temporary wetlands tend to recharge groundwater, seasonal wetlands can have either a recharge or flow-through function, semipermanent wetlands tend to have either a flow-through or discharge function, and saline tend to function mostly as discharge sites.

Chemistry
The chemical characteristics of prairie wetlands also vary in relation to fluctuations in climate and hydrology. Prairie wetlands have dissolved solid concentrations that span the gradient from fresh to extremely saline (LaBaugh 1989). Hydrologic processes, especially those that define how individual wetlands receive and lose water, largely determine the salt concentration of individual wetlands at any given point in time. Wetlands range in specific conductance from 42 (Petri and Larson 1973) to 472,000 μS cm^{-1} (Swanson et al. 1988; LaBaugh 1989), while fluctuations of individual wetlands can range from 1,160 to 43,600 μS cm^{-1} (LaBaugh et al. 1996 and unpublished data). Most wetlands in the PPR are alkaline (pH > 7.4)(LaBaugh 1989), with values as high as 10.4 in North Dakota marshes (Swanson et al. 1988).

Vegetation
Plant communities in prairie wetlands are dynamic and continually changing as a result of short- and long-term fluctuations in water levels, salinity, and anthropogenic disturbance. van der Valk and Davis (1978a) proposed a general model describing how wetland plant communities respond to water level fluctuations due to the wet/dry cycle. Four wetland stages are identified: dry marsh, regenerating marsh, degenerating marsh, and lake marsh.

During drought periods marsh sediments and seed banks are exposed. During this dry marsh phase seeds of many mudflat annual and emergent plant species germinate on exposed mudflats, with annual species usually forming the dominant component (van der Valk and Davis 1976, 1978a, Davis and van der Valk 1978a, Galinato and van der Valk 1986, Welling et al. 1988a,b). When water returns, the annuals are lost but the emergent macrophytes survive and expand by vegetative propagation (i.e., regenerating marsh). Depth and duration of the flooding period, combined with the tolerances of the individual species of macrophytes, will determine how these wetland communities develop. If the wetland experiences only shallow flooding, the emergent macrophytes will eventually dominate the entire wetland. However, prolonged deep-water flooding results in the elimination of emergent macrophytes (i.e., degenerating marsh) due to the direct effects of extended inundation and the expansion of muskrats and their consumption of macrophytes. If water levels remain high, the lake marsh stage is eventually reached. Submersed macrophytes become established and dominate in the open water areas. A drawdown of the wetland will be necessary for reestablishment of emergent macrophytes.

Salinity modifies vegetation responses to water level fluctuations. Increasing salinity results in a loss of diversity, with the most saline wetlands having the fewest plant species (Kantrud et al. 1989). Soil salinity is also very important during the dry marsh phase, regulating the germination of emergent macrophytes on exposed mudflats (Galinato and van der Valk 1986). Kantrud et al. (1989) present information describing the salinity tolerances of many prairie wetland plant species, as well as the predicted changes that may occur as salinity changes over the course of the wet/dry cycle.

Until recently little was known about the algal communities of prairie wetlands or their responses to changes in wetland hydrology (Crumpton 1989, Goldsborough and Robinson 1996, Robinson et al. 1997a,b). Algal biomass may be lower than macrophyte biomass, but their overall productivity may be similar due to high turnover rates (Murkin 1989). Four algal communities are recognized within wetland habitats: epipelon (motile algae inhabiting soft sediments), epiphyton (algae growing on submersed surfaces such as macrophytes), metaphyton (floating or subsurface mats of filamentous algae), and phytoplankton (algae of the water column) (Goldsborough and Robinson 1996). A conceptual model describing wetland stages where each of these four communities is dominant has been developed by Goldsborough and Robinson (1996).

Wetland Classes
A number of wetland classification systems are available (Stewart and Kantrud 1971, Millar 1976, Cowardin et al. 1979, Brinson 1993) but Stewart and Kantrud (1971) is specific to the glaciated prairies. Using Stewart and Kantrud (1971), there are seven wetland classes, based on the vegetational zone occupying the central, deepest part of the wetland basin and occupying at least 5 percent of the total wetland area. The seven vegetational zones identified by Stewart and Kantrud (1971) are the wetland-low-prairie, wet-meadow, shallow-marsh, deep-marsh, permanent-open-water, intermittent-alkali, and fen zones.

Stewart and Kantrud's (1971) wetland classification, while based on vegetational characteristics, reflects differences in water permanence and can be related to the water regime modifiers used by Cowardin et al. (1979). Wet-meadow vegetation (e.g., *Poa palustris, Hordeum jubatum*) dominates areas that typically contain water for several weeks after spring snowmelt. Shallow-marsh vegetation (e.g., *Eleocharis palustris, Carex antherodes*) dominates areas where water typically persists for a few months each spring, and deep-marsh vegetation (e.g., *Typha latifolia, Scirpus acutus*) occupies areas where water persists throughout the year. The permanent-open-water zone, characterized by the lack of vascular plants, dominates the central part of wetlands that rarely dry, even during periods of extended drought.

In terms of total area, wetlands of the temporary (Class II), seasonal (Class III), and semipermanent (Class IV) classes comprise the majority of the wetlands in the PPR (Figure 21.2). Ephemeral (Class I) wetlands, while numerous, are small and are not considered wetlands by Cowardin et al. (1979). Permanent (Class V) and alkali (Class VI) wetlands, although usually large in size, are few in number (Stewart and Kantrud 1971). Fens (Class VII) are not common in the PPR, but their unique biota has raised some concern to preserve existing sites as areas of special ecological significance.
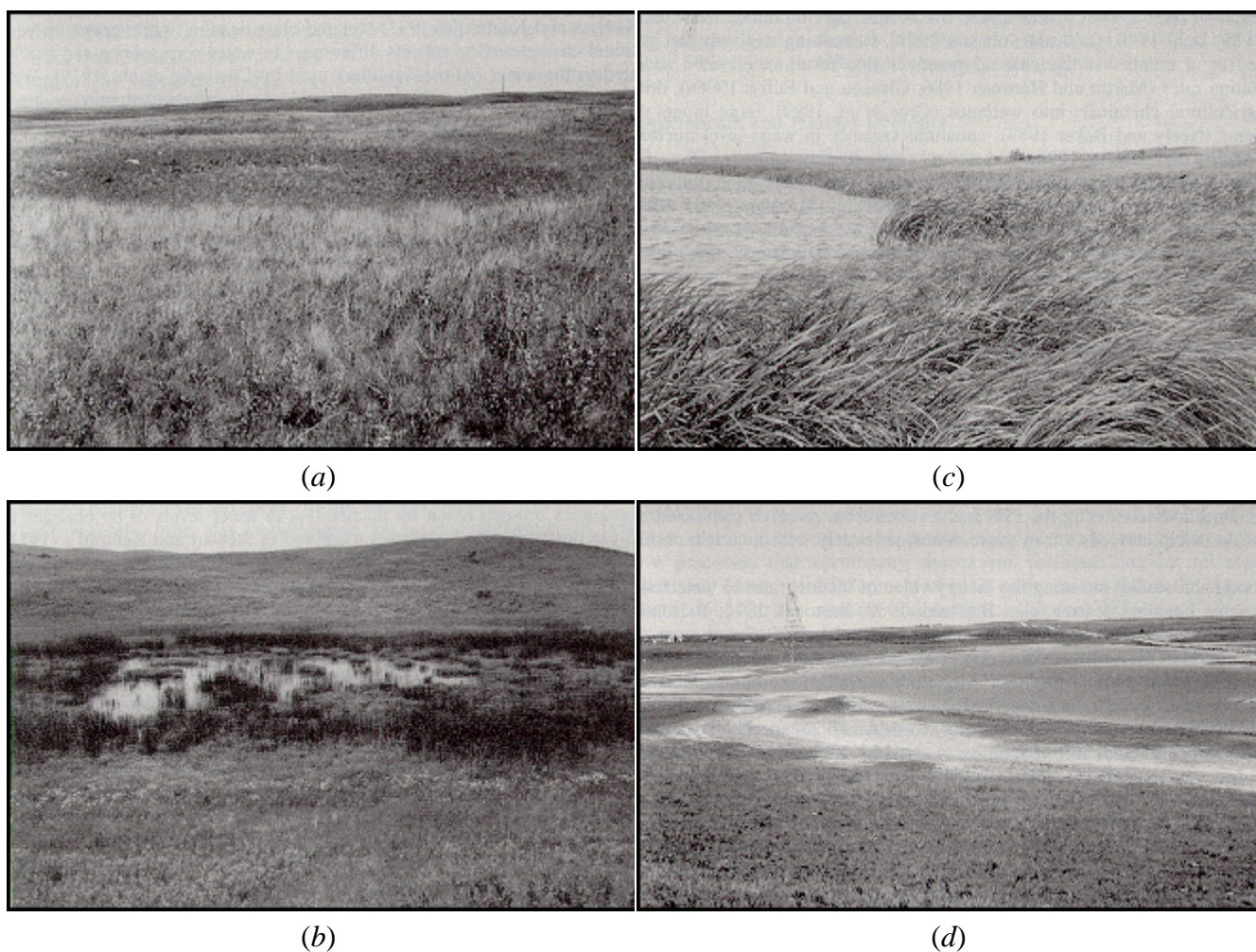

(*a*) (*c*)

(*b*) (*d*)

Figure 21.2. Common wetland classes in the prairie pothole region: (*a*) temporary (Class II); (*b*) seasonal (Class III); (*c*) semipermanent (Class IV); (*d*) alkali (Class VI).

Within wetlands, vegetational zones frequently alternate between two or more distinct phases. These phases are identified by changes in the plant communities brought about by fluctuations in water levels or by changes in land-use practices. The six phases identified in Stewart and Kantrud's (1971) classification are the normal emergent, open-water, drawdown bare-soil, natural drawdown emergent, cropland drawdown, and cropland tillage phases. Although phase changes do not effect wetland classification, they do alter the vegetative structure available to invertebrate communities.

In addition to normal shifts between phases, vegetational zones also shift from one type to another in response to extended drought or above-normal precipitation. If this change occurs in the central, deepest part of a wetland, it can change its classification. During extended drought, wet-meadow vegetation often expands and dominates the central, shallow-marsh zone of seasonal wetlands. Conversely, during extended periods of above normal precipitation, shallow-marsh vegetation frequently expands into the wet-meadow zone. Thus, a seasonal (class III) wetland may shift to a temporary (Class II) wetland; the converse may occur during extended periods of above normal precipitation. As wetlands shift among phases and classes, the characteristic shift in vegetation affects a complimentary shift in the invertebrate community; in general, enhanced vegetative diversity results in an increase in invertebrate richness (Driver 1977).

Landuse Influences
The agricultural value of the PPR has tremendously impacted prairie pothole wetlands. Wetland drainage (both surface and tile) to enhance agricultural production has been the primary factor resulting in the loss of wetlands in this region (Tiner 1984, Canada-United States Steering Committee 1985, Millar 1989, Dahl 1990, Dahl and Johnson 1991). Remaining wetlands are impacted by a number of agricultural practices that result in elevated sedimentation rates (Martin and Hartman 1986, Gleason and Euliss 1996a), drift of agricultural chemicals into wetlands (Grue et al. 1989), large inputs of nutrients (Neely and Baker 1989), unnatural variance in water-level fluctuation (Euliss and Mushet 1996), and altered vegetative communities (Kantrud and Newton 1996). Major nonagricultural impacts include alteration of hydrologic and chemical regimes due to road construction (Swanson et al. 1988) and urban development. The extent to which landuse has altered the ecology of aquatic invertebrates is poorly studied but must be understood to facilitate effective management of prairie wetlands.

Past Invertebrate Research

As pointed out by Rosenberg and Danks (1987), invertebrates of freshwater wetlands are poorly studied and existing information is limited and scattered. As with many other regions in North America, our knowledge of PPR wetland invertebrates is incomplete, but significant work has been conducted, especially over the past several decades. Interestingly, the bulk of our knowledge of wetland invertebrates in the PPR has resulted from research conducted in scientific disciplines other than those concerned solely with invertebrate biology.

Food habit studies stressing the dietary value of invertebrates to waterfowl during the breeding season (e.g., Bartonek 1968, Bartonek 1972, Bartonek and Hickey 1969, Dirschl 1969, Swanson and Bartonek 1970, Swanson et al. 1977) provided the impetus for much of the past research on aquatic invertebrates in prairie pothole wetlands. Migratory waterfowl are of considerable economic value and are the subjects of international treaties. Additionally, the PPR is a critical breeding area for many North American species. As a consequence, much of our information on wetland invertebrates in the PPR has been directed towards developing a better understanding of waterfowl ecology and management. Invertebrate species lists and distribution studies also have significantly contributed to our knowledge of prairie wetland invertebrates but the work has been patchy and is largely incomplete. Overall, basic ecology has provided the smallest contribution to our current knowledge of prairie wetland invertebrates, but development of more holistic perspectives of the critical role that invertebrates play in wetland ecology and function (Murkin and Wrubleski 1988) will likely stimulate such work. Aside from their obvious role in the feeding ecology of waterfowl and other birds, invertebrates provide critical food chain support for a wide variety of other organisms and play significant roles in nutrient cycling and overall wetland productivity (Murkin and Batt 1987). Further, invertebrates are sensitive to agricultural chemicals that accumulate in wetlands (Grue et al. 1989) and there is a growing interest in using them as indicators of wetland and landscape condition in the PPR (Adamus 1996) and elsewhere in the United States.

Invertebrate and Habitat Diversity

There have been relatively few studies providing species lists and habitat distributions of invertebrate fauna in prairie wetlands (Table 21). However, those that have suggest that diversity within specific wetland classes is low in comparison to many other areas of North America. Low diversity is likely attributable to the adverse conditions of the region, including extremely harsh winters and fluctuating hydrology and chemistry. Unlike migratory wildlife, invertebrates inhabiting this area must have adaptations that allow them to withstand these environmental extremes. On a regional scale, however, the overall diversity of invertebrates may be comparable to other areas in North America due to the diversity of wetland classes within the PPR.

Invertebrate Responses to Hydroperiod

The dynamic hydroperiods of prairie wetlands, in relation to both seasonal and the longer-term wet/dry cycle, also exert a positive influence on wetland productivity, including production of aquatic invertebrates. Prolonged inundation results in the decreased availability of plant nutrients whereas oxidative processes that accompany drawdowns facilitate nutrient release and ultimately foster the development of plant communities that make significant contributions to the nutrient and detritus pool upon reflooding. The sharp increase in wetland productivity when wetlands reflood following a dry phase is the reason for artificially flooding and draining wetlands to enhance waterfowl populations (Cook and Powers 1958, Kadlec and Smith 1992) and it is the basis for the modern day practice of

moist soil management (Fredrickson and Taylor 1982). The basic underpinnings of this phenomenon relate to nutrient releases from the aerobic decomposition of accumulated macrophyte litter by terrestrial hyphomycetes (Bärlocher et al. 1978).

Seasonal drawdown, as well as the longer term wet/dry cycle, impacts the hydroperiod of prairie wetlands and has special significance to the ecology of aquatic invertebrates. During extreme drought, nearly all wetlands are dry, including many permanent habitats. Under such conditions invertebrate faunas undergo severe spatial reduction, and they are mostly comprised of specialists that can tolerate hypersaline waters or those that have such short life cycles that reproduction can be completed within an extremely short time. Wetlands can shift hydrologic function during severe drought (Winter and Rosenberry 1995), and viable, but normally dormant, eggs in semipermanent wetlands can hatch producing an invertebrate community that more closely resembles those that characterize temporary or seasonal marshes (Euliss and Mushet, unpublished data), especially when salt concentrations decrease due to deflation (LaBaugh et al. 1996) or dilution from overland flow.

As wetlands refill following drought, wetland invertebrate communities develop along predictable temporal guidelines. As pointed out by Wiggins et al. (1980), the early colonizing invertebrate community is structurally simple and is comprised mostly of r-selected detritivorous invertebrates. Later the invertebrate community becomes more complex as predators and other major functional groups of invertebrates become established as water permanence persists and the habitat becomes more complex in vegetative structure. Reintroduction of invertebrates that cannot tolerate hydroperiods of less than a year (e.g., the amphipods *Hyalella* and *Gammarus*) likely occurs from dispersal on mammals and birds (Segeraträle 1954, Peck 1975, Rosine 1956, Daborn 1976, Swanson 1984). Accompanying with this successional pattern are changes in the spatial distribution and abundance of invertebrates as water permanence persists. For example, fairy shrimp are very abundant during the initial reflooding of semipermanent wetlands but their numbers drop considerably as the hydroperiod lengthens (Euliss and Mushet, unpublished data). Like mosquitoes, fairy shrimp are vulnerable to predation by carnivorous insects in structurally complex communities (Pennak 1989). Increased invertebrate diversity associated with increased water permanence was noted by Driver (1977), who used chironomid diversity to separate wetland classes of prairie potholes in Canada and by Euliss et al. (unpublished data) who used recalcitrant remains of invertebrates to identify, classify, and delineate wetlands in the PPR.

Invertebrate Responses to Salinity
Some aquatic insects inhabiting prairie wetlands are adapted to a wide range of salt concentrations, while others have narrow tolerances. Insect taxa that tolerate wide variations in salt concentrations are the most common and widely distributed in prairie wetlands. Most adult Coleoptera and Hemiptera can withstand a wide range in salinity and are well adapted to exploit the spatial and temporal dynamics of prairie wetlands. Exposure to habitats with unsuitable features such as an unfavorable salinities is avoided by flight. Larval insects and noninsect invertebrates that cannot fly must rely on other adaptations to facilitate survival under adverse conditions.

Nonflying invertebrates possess a different suite of adaptations that have allowed them to exploit highly productive saline prairie wetlands. Adaptations may include eggs and cysts, waterproof secretions, burrowing into substrates, and physiological adaptations (Scudder 1987). Swanson et al. (1988) reports that *Lymnaea stagnalis* was the dominant gastropod in permanent or semipermanent wetlands having specific conductances of <5,000 µS cm-1. However, as salt concentrations exceeded 5,000 µS cm^{-1}, *Lymnaea elodes* replaced *Lymnaea stagnalis* but was unable to persist at higher

concentrations (>10,000 µS cm^{-1}). Similarly, anostracans like *Branchinecta lindahli* are common invertebrates in seasonal and semipermanent wetlands in the initial stages of the wet/dry cycle when salt concentrations are low (Euliss and Mushet, unpublished data), but they cannot tolerate extremely high salt concentrations that develop in the drought stage of the wet/dry cycle. At salt concentrations >35,000 µS cm^{-1}, the anostracan fauna may shift entirely to the brine shrimp, *Artemia salina* (Swanson et al. 1988). Amphipods are common in semipermanent and permanent wetlands of intermediate salinity; most species are found in waters of low or medium carbonate content (Pennak 1989). Insects also show this trend, with most taxa giving way to brine flies (Ephydridae) and certain water boatmen at higher salt concentrations. Increasing salt typically results in lower diversity, although the productivity of the few specialists capable of tolerating the osmotic stress may be high (Euliss et al. 1991).

Invertebrate Responses to Vegetation

Habitat structure provided by hydrophytes changes between years and within seasons as plant communities respond to hydrology, climate, and human alterations. Different invertebrate communities are often associated with different plant species or plant communities (e.g., Voigts 1976, McCrady et al. 1986, Wrubleski 1987, Olson et al. 1995). Macrophytes increase habitat structural complexity, providing additional food and living space within the water column for species that would otherwise not be present (e.g., Berg 1949, 1950, Krull 1970, Gilinsky 1984, Bergey et al. 1992). These plants 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). By increasing structural habitat complexity, these plants also modify predator-prey interactions (e.g., Rabe and Gibson 1984, Gilinsky 1984, Batzer and Resh 1991).

Areas with aquatic macrophytes have been reported to support higher numbers of invertebrates than bare areas (Gerking 1957, 1962, Krull 1970). However, Olson et al. (1995) found that nektonic invertebrates were more numerous in open water areas with dense filamentous algae, but biomass was greater in *Typha* stands. Wrubleski (1991) observed no difference in insect emergence between areas with and without submersed macrophytes. Voigts (1976) reported that invertebrate groups respond differently to changes in macrophyte communities, but in general, maximum numbers of aquatic invertebrates occurred where beds of submersed vegetation were interspersed with emergent vegetation. As the aquatic macrophyte communities change as a result of natural or anthropogenic alterations, so do their associated aquatic invertebrate communities (Driver 1977, Wrubleski 1991, Hanson and Butler 1994).

Aside from increasing the amount of habitat available to aquatic invertebrates, aquatic macrophytes also contribute to marked changes in the physical and chemical environment. These changes, in turn, may modify invertebrate responses to vegetation and the habitat they provide. Macrophytes restrict water circulation and contribute to gradients in light, temperature, and dissolved oxygen in very shallow standing waters (e.g., Kollman and Wali 1976, Carpenter and Lodge 1986, Rose and Crumpton 1996). Anoxic conditions can prevail within stands of emergent vegetation (Suthers and Gee 1986, Rose and Crumpton 1996) or beneath beds of submersed macrophytes (Kollman and Wali 1976), and this can impact invertebrate abundance, movement, and behavior (e.g., Murkin and Kadlec 1986a, Murkin et al. 1992).

Invertebrate Responses to Weather
Temperature. Winters in the PPR are very cold, and many shallow-water bodies freeze completely. These habitats have been referred to as "aestival ponds" (Welch 1952, Daborn and Clifford 1974). They are effectively winter-dry habitats, differing from other temporary aquatic habitats, because the dry phase is a function of temperature rather than water supply; all biological activity is restricted to the summer period. The severity of freezing varies greatly between years and is dependant upon water depth, snow cover and the extent of low temperatures (Danks 1971a, Daborn and Clifford 1974), and this in turn can impact invertebrate community structure. The amphipods *Hyalella* and *Gammarus*, for example, are not found in wetlands that freeze completely (Daborn 1969). However, the relative importance of freezing and overwintering on invertebrate communities in these habitats has received little attention.

Many wetland invertebrates avoid the risk of freezing by migrating to habitats that do not freeze completely. Most Hemiptera and Coleoptera overwinter as adults, and many migrate from shallow habitats to deeper ponds and lakes (Danks 1978). However, Danell (1981) did recover a live corixid and an adult beetle from the frozen ice and the upper part of the frozen bottom sediments of a shallow lake in northern Sweden. Water striders (*Gerris* spp.) overwinter as adults in terrestrial vegetation adjacent to ponds, frequently in aggregations (Nummelin and Vespalainen 1982). Some mosquitoes also overwinter as adults (*Culiseta, Culex, and Anopheles* spp.) in rodent burrows, hollow trees, and unheated buildings (Wood et al. 1979).

In wetlands that do not freeze solid, some invertebrates will move to deeper water to avoid freezing. Several studies have reported invertebrate movements to deeper water habitats in the fall (Wodsedalek 1912, Eggleton 1931, Moon 1935, 1940, Gibbs 1979, Davies and Everett 1977, Boag 1981). However, those invertebrates that migrate to areas that do not freeze may experience potentially harmful anoxic conditions and increased levels of hydrogen sulfide and other toxic dissolved substances (Daborn and Clifford 1974, Danks 1971a). Invertebrate adaptations to these conditions include anaerobic metabolism (Reddy and Davies 1993), reduced activity and feeding (Davies and Gates 1991), and movement to microhabitats offering better conditions (Brittain and Nagell 1981).

Those invertebrates that do not migrate must posses a means of tolerating freezing conditions. This is accomplished physiologically through freezing resistance (avoiding freezing) or freezing tolerance (Block 1991, Duman et al. 1991). Many benthic invertebrates are able, while encased in ice, to resist freezing by means of supercooling and the production of various antifreeze agents. Daborn (1971) and Sawchyn and Gillott (1975) both describe how coenagrionid damselflies were collected encased in ice, but were not frozen. Freeze-tolerant invertebrates are those that can survive extracellular ice formation within their bodies. Chironomids are a well-known example of this group (Danks 1971b).

Snow insulates and protects wetland invertebrates from the severe temperatures experienced above the ice (Danks 1971b). Emergent vegetation is important in holding this snow. Therefore removal of emergent vegetation would result in lower temperatures and possibly greater invertebrate mortality (Dineen 1953). Sawchyn and Gillott (1974a) reported that adequate snow cover was necessary to prevent egg mortality in three species of *Lestes* damselflies. Sawchyn and Gillott (1975) suggested that overwintering mortality of coenagrionid damselfly nymphs observed by Daborn (1969, 1971) may have been due to lethal ice temperatures caused by an absence of snow cover. Further research is needed to determine how important overwintering conditions are in structuring PPR wetland invertebrate communities and the role that vegetation plays in mitigating temperature extremes.

Wind and Rain. Weather can be an important factor modifying wetland invertebrate activity and behavior. Inclement weather can reduce emergence of adult chironomids and other insects (Swanson and Sargeant 1972, Wrubleski and Ross 1989), and can force flying insects to seek shelter in stands of emergent vegetation (King and Wrubleski 1998). Rasmussen (1983) reports that windy, rainy weather conditions during the emergence period resulted in a reduction in mating and the subsequent production of chironomid larvae in a prairie pond. Reductions in invertebrate abundances or activity will impact the foraging behavior and survival of waterfowl, particularly the youngest ducklings, which are dependant upon flying insects as an important food resource (Chura 1961, Sugden 1973, Roy 1995, Cox et al. 1998).

Invertebrate Responses to Anthropogenic Disturbances
The PPR is far different today than presettlement times, primarily because of modern agriculture. Agricultural activities on the uplands that surround prairie wetlands have impacted and altered aquatic invertebrate communities. Agrichemicals are the most obvious anthropogenic influence, and they have been shown to cause significant mortality in aquatic invertebrates (Borthwick 1988, Grue et al. 1989). Less obvious, however, are the physical effects related to cultivation, erosion, and sedimentation. Euliss and Mushet (unpublished data) found that *Cladocera ephippia* were less abundant in the tilled basins of temporary wetlands in agricultural fields compared to wetlands in grassland landscapes with no prior tillage history. Suspended silt and clay are known to be toxic to zooplankton and to reduce the foraging and assimilation rate of food items consumed by invertebrates (Robinson 1957, McCabe and O'Brien 1983, Newcombe and McDonald 1991). Other sediment effects include the clogging of filtering apparatuses, impacts on aquatic food chains through shading and covering of primary producers (Gleason and Euliss 1996b), and the burial of associated seed banks (Jurik et al. 1994; Wang et al. 1994). Although poorly studied, the burial of invertebrate eggs by sediments washing into wetlands may exert a significant influence on wetland invertebrate communities. Even seemingly innocuous influences like haying and burning of wetlands may negatively impact invertebrates if the vegetation is removed late in the growing season. As noted above, emergent vegetation holds snow, which provides thermal cover to protect invertebrates from severe freezing conditions. Wetland drainage, another landuse associated with agriculture, has focused mostly on shallow temporary and seasonal wetlands within agricultural fields. The result has been a shift in the proportion of available wetland classes and alteration of hydrologic regimes of many nondrained wetlands. The nonintegrated PPR watersheds facilitated the drainage of shallow wetlands into larger semipermanent wetlands resulting in semipermanent wetlands, that are much deeper and more expansive than in pristine times. Lastly, road construction has severely altered the chemical and hydrologic characteristics of prairie potholes, the most important to invertebrates being the creation of hypersaline wetlands when construction projects isolate areas of wetlands from groundwater inflow (Swanson et al. 1988).

Recolonization and Dispersal Mechanisms
Recolonization and dispersal mechanisms for prairie pothole invertebrates are poorly studied, but clearly the dynamic and harsh environmental conditions of the area has influenced this region's naturally low invertebrate diversity. Flight is one of the most important dispersal mechanisms of insects. Flying insects rapidly disperse into temporary and seasonal wetlands following normal seasonal flooding, but the recolonization of wetlands following extreme drought may be slower because fewer flooded wetlands during the drought are available to provide refugia for recolonizing stocks (Swanson 1984).

Flightless life stages of insects and noninsectan invertebrates face even greater challenges to recolonize previously dry wetlands. Common recolonization mechanisms include eggs and cysts resistant to drying and freezing, diapause, aestivation, waterproof secretions, epiphragms (snails), burrowing, and even the use of invertebrate and vertebrate wildlife. Wiggins et al. (1980) outlined a temporal sequence, strongly influenced by climatic conditions, in which various taxa of invertebrates invade newly flooded habitats, using a variety of recolonization mechanisms. In general, the diversity of invertebrates is low because relatively few taxa possess the necessary physiological or behavioral adaptations that allow them to exploit the rich food resources available in prairie wetlands. Such systems favor ecological generalists that are early colonizers and exploit resources unavailable to other taxa lacking the necessary adaptations. The temporal sequence involves early detritivorous invertebrates with mostly r-selected characteristics and later support predatory invertebrates that recolonize habitats that persist for a sufficient length of time.

Passive dispersal mechanisms are important they include dispersal by wind (Pennak 1989), by being carried in the digestive tracts of birds (Proctor 1964, Proctor et al. 1967, Swanson 1984), and by clinging to more mobile fauna. Ostracods and clams have been observed clinging to migrating Hemiptera and Coleoptera (Fryer 1974) and amphipods can be carried in the feathers of waterfowl (Segerströle 1954, Rosine 1956, Swanson 1984). Peck (1975) observed *Hyalella azteca* and *Gammarus lacustris* on the fur of muskrat (*Ondatra zibethicus*) and beaver (*Castor canadensis*). Although not documented, epizoochory is a common means of seed dispersal on feathers of waterfowl and it is conceivable that invertebrate propagules are transported in that fashion as well. Cladocera ephippia float on the waters surface and sometimes form extensive mats. Some ephippia have elaborate appendages that may facilitate adhesion to feathers as has been described for epizoochory on the feathers of waterfowl (Vivian-Smith and Stiles 1994). However, wetland drainage increases the distance between wetlands and may disrupt transporting mechanisms or delay introductions.

Biotic Interactions

Aquatic Macrophytes and Algae

Herbivory by aquatic invertebrates on macrophytes has generally been reported to be unimportant (Crow and Macdonald 1978, Polunin 1984, Mann 1988), although this view has been questioned by Lodge (1991) and Newman (1991). Isolated accounts of terrestrial insect damage to wetland macrophytes have been reported (e.g., van der Valk and Davis 1978b, Klopatek and Stearns 1978, Penko and Pratt 1986, 1987, Sheldon 1987, Foote et al. 1988). At the Woodworth Study Area (Higgins et al. 1992) in south-central North Dakota, *Polygonum amphibium* was observed to be heavily grazed by the chrysomelid beetle *Galerucella nymphaeae* (Wrubleski and Detenbeck in prep.). Two European *Galerucella* species, *calmariensis* and *pusilla*, are currently being released as biocontrol agents for the introduced *Lythrium salicaria* (Malecki et al. 1993).

Although the relative extent of macrophyte herbivory is not well documented in prairie pothole wetlands, it is generally recognized that most macrophyte production eventually ends up as detritus (Davis and van der Valk 1978b). The abundant production of detritus may be the most important source of nutrients and energy for the invertebrates in wetland habitats (Mann 1988, Murkin 1989). Either through direct consumption of decaying macrophyte tissue or the consumption of associated microbial fauna, this litter is generally thought to be extremely important to wetland invertebrates (Mann 1988). However, recent stable isotope studies have indicated that algae may be a more important food resource for invertebrates than macrophyte litter. Neill and Cornwell (1992) present evidence, based on stble isotope signatures, that aquatic macrophytes were not important sources of carbon for aquatic invertebrates in the Delta Marsh. This has been confirmed by a recent study in wetlands at the Woodworth Study Area (Wrubleski and Detenbeck, in prep.). $\delta^{13}C$ signatures for most aquatic invertebrates closely matched algae, but not macrophytes (Fig. 21.3). This has been confirmed by a recent study by Wrubleski and Detenbeck (in prep.). Except for epipelon, $\delta^{13}C$ signatures of algae were more deplete (more negative) than the aquatic macrophytes (Fig. 21.3). Most aquatic invertebrates also had $\delta^{13}C$ signatures that were more deplete than the macrophytes and closely matched the algal $\delta^{13}C$ signatures, indicating their reliance upon algae as their principal source of carbon.
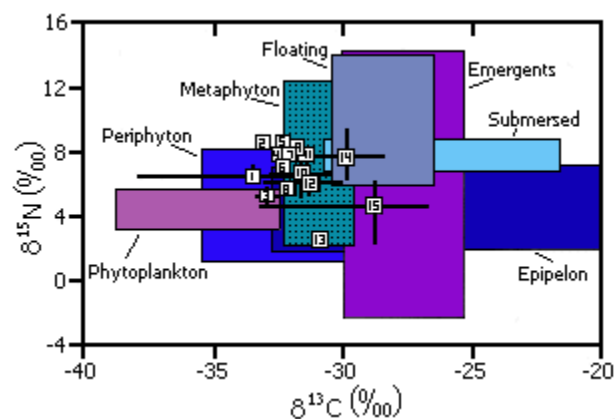

Fig. 21.3. Stable carbon and nitrogen isotope ratios for the algae, macrophytes, and aquatic invertebrates sampled in 10 wetlands at the Woodworth Study Area, North Dakota, 1994-95. Shaded boxes for the algae (phytoplankton, periphyton, epipelon, and metaphyton) and macrophytes (floating, emergents, and submersed) represent the complete range of values obtained. Mean and ranges are presented for the following aquatic invertebrates: 1, Cladocera; 2, copeppods; 3, *Glyptotendipes*; 4, Tanypodinae; 5, Hydracarina; 6, Ephemeroptera; 7, Chaoboridae; 8, *Chironomus*; 9, Zygoptera; 10, Corixidae; 11, Notonectidae; 12, Dytiscidae; 13, Hydrophilidae; 14, Anisoptera; and 15, Gastropoda.

Algal communities in prairie wetlands have generally been ignored (Crumpton 1989, Murkin 1989, Goldsborough and Robinson 1996), and consequently the effects of herbivory on algae have not been studied. In other wetland habitats invertebrate grazing has been found to be important in structuring algal communities and overall productivity (Cattaneo 1983, Hann 1991, Botts 1993). The relative importance of the different algal communities is unknown. Metaphyton has been reported to be an important habitat for many aquatic invertebrates (Ross and Murkin 1993, Olson et al. 1995), but does not appear to be a food resource (Goldsborough and Robinson 1996). Evidence from stable isotopes suggests that phytoplankton and periphyton are important food resources to aquatic invertebrates during the summer period (Wrubleski and Detenbeck, in prep.). More effort is needed to determine the relative importance of each algal community, and how these values change over seasonal and longer-term wetland cycles.

Trophic Functions of Invertebrates in Prairie Wetlands
Invertebrates are widely recognized as an important food resource for waterfowl and other aquatic birds (see reviews by Murkin and Batt 1987, Swanson and Duebbert 1989, Krapu and Reinecke 1992, Sedinger 1992). They supply the necessary proteins and lipids for successful production of eggs by hens and for growth by ducklings (Swanson et al. 1974, 1977, Driver et. al. 1974, Krapu 1979). Invertebrates are rich in protein and several essential amino acids that cannot be obtained from plants or seeds (Sugden 1973, Driver et al. 1974). They are also excellent sources of lipids and energy (Driver et al. 1974, Driver 1981, Afton and Ankney 1991). Due to their importance to waterfowl, invertebrate abundances can influence wetland use and feeding behavior (Kaminski and Prince 1981, Talent et al. 1982, Murkin and Kadlec 1986b, Sedinger 1992).

Aside from waterfowl, aquatic invertebrates are important food resources for passerines (Willson 1966, Mott et al. 1972, Voigts 1973, Twedt et al. 1991), shorebirds (Eldridge 1987), grebes, and other wetland birds. Adult aquatic insects (e.g., chironomids, dragonflies, mayflies) originating from wetland habitats provide an important food resource for many nonwetland birds as well (Busby and Sealy 1979, Sealy 1980, Guinan and Sealy 1987).

Tiger salamanders are a common amphibian found in prairie wetlands (Larson 1968, Buchli 1969, Deutschman 1984, Pterka 1987). Olenick and Gee (1981) reported that tiger salamanders were benthic and fed primarily on *Gammarus*. Deutschman (1984) reports that tiger salamanders mostly consumed Cladocera, chironomids, amphipods, ephemeropterans, and hemipterans and that larger prey (i.e., large amphipods and chironomids) were preferred over smaller prey such as cladocerans and copepods. While the consumption of large prey maximizes growth (Deutschman 1984), it is likely that most large invertebrates are consumed when they are available in prairie wetlands. At night, tiger salamanders float up in the water column to feed on invertebrates (Anderson and Graham 1967, Branch and Altig 1981). They use deep portions of wetlands as refugia from avian predators during the day. Much of the nocturnal movement of tiger salamanders is apparently from the center and deeper portion of wetlands towards the shoreline. Lannoo (unpublished data) found that funnel traps with openings oriented towards the deeper wetland center caught twice the number of salamanders as traps with openings oriented parallel to the shoreline. Interestingly, Corkum (1984) notes that over 60 percent of the movements of aquatic invertebrates also occurred at night and towards the deeper water of the wetland center.

Conditions in most prairie wetlands are not favorable for fish (Peterka 1989). Frequent drying, nonintegrated watersheds, and harsh winter conditions generally prevent fish from establishing permanent populations. However, they can become established through deliberate introductions. For example, fathead minnows (*Pimphales promealas*) are released in wetlands for rearing by the baitfish industry (Hanson and Riggs 1995), and rainbow trout (*Salmo gairdneri*) are released for sport and commercial harvest (Peterka 1989). As in other aquatic habitats, fish can be very important predators of aquatic invertebrates and potentially compete with waterfowl and other marsh birds for food (Swanson and Nelson 1970). Hanson and Riggs (1995) report marked reductions in invertebrate abundance, biomass, and taxa richness in wetlands stocked with fathead minnows. Recently, Bouffard and Hanson (1997) have concluded that fish in wetlands were incompatible with objectives established for waterfowl management, primarily due to the negative impact of fish on invertebrate communities.

Leeches, dragonflies, beetles, and other predaceous invertebrates are abundant in prairie wetlands, but there have been few studies of predator-prey relationships and competition among aquatic invertebrates within these habitats. The importance of these interactions in other aquatic habitats is widely recognized (e.g., Bay 1974, Kerfoot and Sih 1987). In prairie wetlands vertebrate predators such as fish are often absent, making predaceous invertebrates the top aquatic predators. Anderson and Raasveldt (1974) reported that *Gammarus* and *Chaoborus* were important predators of zooplankton in prairie lakes and ponds. Rasmussen and Downing (1988) observed that the spatial distributions of benthic dwelling chironomids were determined by the presence of the predatory leech, *Nephelopsis obscura*. Clearly, invertebrate predators may play an important role in structuring wetland invertebrate communities, but further research is needed to determine their relative importance.

Ecological Functions of Invertebrates in Prairie Wetlands
Aquatic invertebrates in prairie wetlands probably perform ecological functions similar to those documented in other shallow water habitats (Murkin and Wrubleski 1988). The trophic importance of aquatic invertebrates has been elaborated above, but other ecological functions are not as well known or studied. Benthic invertebrates influence sediment chemistry, structure, and nutrient dynamics (Gallepp 1979, Graneli 1979, Gardner et al. 1981, 1983). Their burrowing and mixing activities within the sediments can potentially impact seeds and seedling establishment of aquatic macrophytes (Grace 1984).

Aquatic invertebrates are often assumed to play a major role in decompositional pathways in wetlands (Polunin 1984, Mann 1988). However, there is relatively little evidence to support this assumption other than some generalized knowledge of feeding habits for some groups. In a study of macrophyte litter decomposition in the Delta Marsh, Bicknese (1987) reports that aquatic invertebrates had little influence on litter decomposition dynamics. This was further corroborated with stable isotope evidence which indicates that most invertebrates, are not feeding on wetland macrophyte detritus (Neill and Cornwell 1992; Wrubleski and Detenbeck, in prep.). Mining and burrowing activities by invertebrates within litter undoubtedly contribute to increased litter decomposition, but direct consumption does not appear to be important.

Wetlands are often regarded as sources of insect pests such as mosquitoes, horseflies, and deerflies. Most mosquito production in the PPR actually originates from temporary snowmelt and rain pools. For example, *Aedes* spp. lay their eggs in shallow dry depressions, and the eggs which hatch only when flooded by snowmelt or rainwater (Wood et al. 1979). One mosquito that does occur in more permanent waters and is of concern is *Culex tarsalis*. This species is the principal vector of western equine encephalitis, a serious viral disease for horses and humans (Wood et al. 1979).

Leeches are common ectoparasites on waterfowl (Trauger and Bartonek 1977). Amphipods, snails, leeches, and other wetland invertebrates act as intermediate hosts for a variety of bird intestinal parasites (e.g., LaBerge and McLaughlin 1989). Biting flies are also vectors of a variety of blood parasites for marsh birds (e.g., Meyer et al. 1974, Bennett et al. 1982). The relative impact of these parasites on wetland bird mortality is not well known (Sargeant and Raveling 1992).

Conceptual Framework for Research and Management

Considering the dynamic climate, hydrology, and chemistry of the prairies, it is significant that past research has shown no evidence that wetland invertebrates have developed adaptations specific to the PPR. Rather, the available evidence suggests that systems such as the PPR have a naturally low diversity of invertebrate fauna, comprised mostly of ecological generalists. Those taxa present already possessed the necessary physiological and behavioral adaptations needed to exploit the rich food resources of prairie wetlands (Wiggins et al. 1980). In support of this concept, Hamrum et al. (1971) reports low diversity of dragonflies in the PPR of western Minnesota relative to wetlands in eastern Minnesota outside of the PPR. Low diversity and no endemic species of odonates are also reported by Bick et al. (1977) for the Dakotas, and they conclud that the fauna was primarily (49 percent) transcontinental with many northern species. Apparently, the Dakotas represent a greater obstacle to the northward movement of species than the converse.

The general characteristics of prairie pothole invertebrates and the dynamic nature of prairie wetlands warrant special consideration to facilitate effective research and conservation efforts. The critical roles that climate and parent geology has on wetland hydrology, hydroperiods, chemistry, and ultimately the biota needs to be considered by both managers and scientists. Taxa that utilize prairie wetlands face seasonal dewatering, increasing osmotic tensions as salts concentrate, and winter temperatures that solidly freeze many prairie wetlands. On a broader temporal scale, invertebrates must be able to maintain populations in the face of long-term drought that often results in many wetlands being entirely dry. Recolonization often occurs from limited refugia, and many different adaptations have enabled invertebrates to withstand the rigors of the PPR.

It is important that researchers and managers work within a framework that considers the impact of the dynamic climate, hydrology, and chemistry on prairie wetland biota. Studies or conservation efforts that do not consider the spatial variability of wetlands (i.e. different chemical and biological characteristics of wetlands due to different hydrologic functions) will have a low probability of yielding satisfactory results as will efforts that do not consider temporal variability (i.e., annual freezing, seasonal drawdowns, and widespread drawdowns in relation to long-term drought). Because the normal wet/dry cycle of the PPR is on a 10-20 year schedule (Duvick and Blasing 1981, Karl and Koscielny 1982, Karl and Riebsame 1984, Diaz 1983, 1986), it is clear that long-term research projects are needed to develop a complete understanding of how these systems function and how wetland invertebrates respond. Alternatively, researchers conducting shorter-term studies need to carefully define the class of wetland(s) studied, their basic chemical characteristics (a measure of salinity at a minimum), their vegetative characteristics, and if possible, their hydrologic function. Finally they need to define the time frame of their studies within the context of the wet/dry cycle.

Likewise, managers of prairie wetlands need to manage their wetlands within the context of the long-term drought cycle. Periodic drawdown and oxidation of sediments is a natural process that is necessary to maximize the overall productivity of prairie wetlands. Managed wetlands are frequently drawn down to enhance production for waterfowl populations (Cook and Powers 1958, Fredrickson and Taylor 1982, Kadlec and Smith 1992). Such management also benefits invertebrates when wetlands are reflooded, due to nutrient release and its effect on primary production. Additionally, vegetation growing in dry wetland basins provides an additional source of nutrients, substrate, and fresh carbon for the detritus pool when reflooded. Despite this knowledge, however, most restored and constructed wetlands in the PPR do not have water control structures and hence are totally dependent upon natural wet/dry cycles to rejuvenate wetland productivity. In addition, many managed wetlands

that have water control structures are not drawn down frequently enough to mimic the natural drought cycle and enhance productivity of invertebrates and other biota (Leigh Fredrickson, personal communication). Others, such as the Delta Marsh in south-central Manitoba, have stabilized water levels that have resulted in reduced wetland productivity and value as wildlife habitat (Batt in press.). Future research and management of PPR wetlands needs to focus more intensively on maximizing wetland functions, including the production of aquatic invertebrates, to offset prior wetland losses (Bellrose and Low 1978).

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