Chapter 8

Invertebrates in Permanent Wetlands (Long-Hydroperiod Marshes and Shallow Lakes)

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Introduction to Permanent Wetlands (Long-Hydroperiod Marshes and Shallow Lakes)

Habitat Attributes

Permanent wetlands are probably best viewed as waters existing along a continuum resulting from gradients of biological, chemical, and physical features and occurring between shallow wetlands that periodically dry and deeper lakes. Rigorous global classification of permanent wetlands has proven difficult for many reasons (Finlayson and Van der Valk 1995). Classification systems allowing for regional or even national inventories are often impossible to apply internationally due to broader patterns of habitat variability and unique nature of regional aquatic systems. Also, shallow freshwaters have highly variable origins, geomorphology, nature and extent of ground-water interactions and flow networks, and often comprise portions of larger more complex lake and wetland habitats. Still, it is worthwhile to apply classification systems to link waters defined here, because classification approaches are widely applied by habitat managers, and because we believe it is important that practitioners understand which aquatic habitats support the invertebrate communities we describe.

For this review, we are narrowing our focus to permanently flooded wetlands, and defining these as lentic freshwaters with relatively shallow maximum depth (usually <4 m, Scheffer 2004), yet presence of standing water during all but extreme droughts (such as that experienced in North America during the 1930s). Lakeshore marshes are covered in another chapter of this book, but we do include some examples of habitats that exchange waters with, and comprise portions of, much larger systems, but are of sufficient size or isolation to develop unique characteristics making them distinct from adjacent lakes.

The classification system described by Cowardin et al. (1979) is especially useful here because it recognizes a continuum of waters and has application to

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shallow ecosystems worldwide. Our focus here is on palustrine and lacustrine systems, but we limit these to include only waters defined as littoral (not limnetic) in the Cowardin approach (hereafter permanent wetlands). From an international perspective, these are the habitats classified as lacustrine or shallow water marshes by Warner and Rubec (1997) or as permanent fresh marshes/pools following the international Ramsar Convention (Matthews and Townsend 1993). These permanent wetlands include a wide range of substrates from unconsolidated organic matter to rocky bottoms, emergent and submergent aquatic macrophytes, and a wide range of adjacent upland vegetation from grassland to coniferous forest. Our definition also includes a range of conditions with respect to hydrologic exchange with underlying groundwater, but hydrologic relationships are often poorly known, even for permanent wetlands that have received considerable study.

Our habitat definition is also guided by our conviction that what makes biological communities in these waters unique is the influence of three fundamental properties; together, these attributes establish ecosystem characteristics of permanent wetlands. First, these waters are relatively shallow, in many cases mean depths are <1.5 m. This contributes to the second major property; shallow depth prevents stratification so these waters remain polymictic throughout open-water periods in north-temperate regions, and year-round in mid- and southern latitudes. And finally, sunlight reaches large portions of substrates at levels sufficient to stimulate growth of submergent and emergent vascular plants across the majority of the basin. A grouping of waters based on these features results in a habitat category that spans an extraordinarily wide range of size, geomorphology, and origins, and general examples of these are explained in more detail below. However, we emphasize that understanding factors affecting aquatic invertebrate communities in these ecosystems requires a functional classification that relies heavily on depth, polymixis, and potential for colonization by aquatic macrophytes. In a sense, this is a broad permanent wetland classification with ragged ecological edges, but such an approach is necessary in order to elucidate common factors structuring ecological communities in these waters.

We also recognize that, as Wiggins et al. (1980) and Wellborn et al. (1996) suggested, freshwaters may be ranked along a continuum of habitat permanence and predation potential, and that these two factors work concurrently to establish the importance of other environmental and biological variables structuring resident communities. Following the conceptual framework of Wellborn et al. (1996), we further define permanent wetlands as freshwaters with sufficient depth to sustain permanent aquatic communities, yet encompassing a key ecological transition: these areas may or may not support populations of fish. Here then, permanent wetlands are waters supporting aquatic invertebrate communities that are subject to a variety of predation conditions ranging from only invertebrate predators, to habitats that occasionally include fish, to waters that support permanent fish communities. Throughout north-temperate regions, many of these areas are ice-covered for up to 5–6 months each year. Winter conditions favor prolonged periods of under-ice hypoxia and this sometimes reduces, or even eliminates, fish populations (Peterka

1989). Still, fish predation is among the most important properties structuring aquatic invertebrate communities in permanent wetlands (Zimmer et al. 2000; Hanson et al. 2005).

Geographic Distribution of Permanent Wetlands

Freshwater permanent wetlands are widespread, and the scientific literature indicates that these areas comprise a major global habitat resource for aquatic invertebrates. Permanent wetlands in modern landscapes have been formed by a wide variety of physical processes operating at different temporal and spatial scales. Many permanent wetlands are the direct result of anthropogenic activities; some of the best known of these are wetlands formed by flooding in ancient excavations in the Netherlands, or from water filling ditches and abandoned mining sites in the United Kingdom (Moss et al. 1996; Scheffer 2004). On the other hand, naturally occurring permanent wetlands are probably far more widespread and are a result of a variety of natural processes ranging from precipitation and groundwater filling depressions left behind by retreating glaciers in North America (Kantrud et al. 1989) to extreme flooding events that permanently inundated a vast area previously comprising coastal lowlands in southeastern China (Qin et al. 2007).

As with other freshwater wetlands, characterizing permanent wetland features is difficult because regionally unique combinations of climate, water availability, soils and underlying geological substrates, and other factors contribute to extreme variability in biological, chemical, and physical features of these waters worldwide. Comprehensive descriptions of permanent wetlands from many geographical settings are beyond the scope of this chapter, but examples are useful to illustrate variability and to show how environmental variables may structure aquatic invertebrate communities in these habitats. As a starting point, hydrology is a common structuring factor and a key determinant of wetland characteristics. Hydrology, in turn, interacts with other local, regional, and even continental influences. Resulting among-wetland variability is extraordinary and invertebrate communities may differ sharply in response to water quality and chemistry gradients resulting from different hydrologic relationships (Kantrud et al. 1989) (Fig. 8.1).

For example, throughout the Prairie Pothole Region (PPR) of north-central United States and south-central Canada, thousands of permanent wetlands remain within depressions underlain by soils originating from variable depths of till left behind by retreating glaciers (Kantrud et al. 1989). A negative water balance characterizes most of the region, as annual rates of evapotranspiration usually exceed precipitation. Along with highly variable morainic topography, partially impermeable glacial till (up to 250 m deep in some locations) contributes to complex flow networks and intense interactions between surface and underlying groundwater with combinations of recharge, flow-through, and dis-

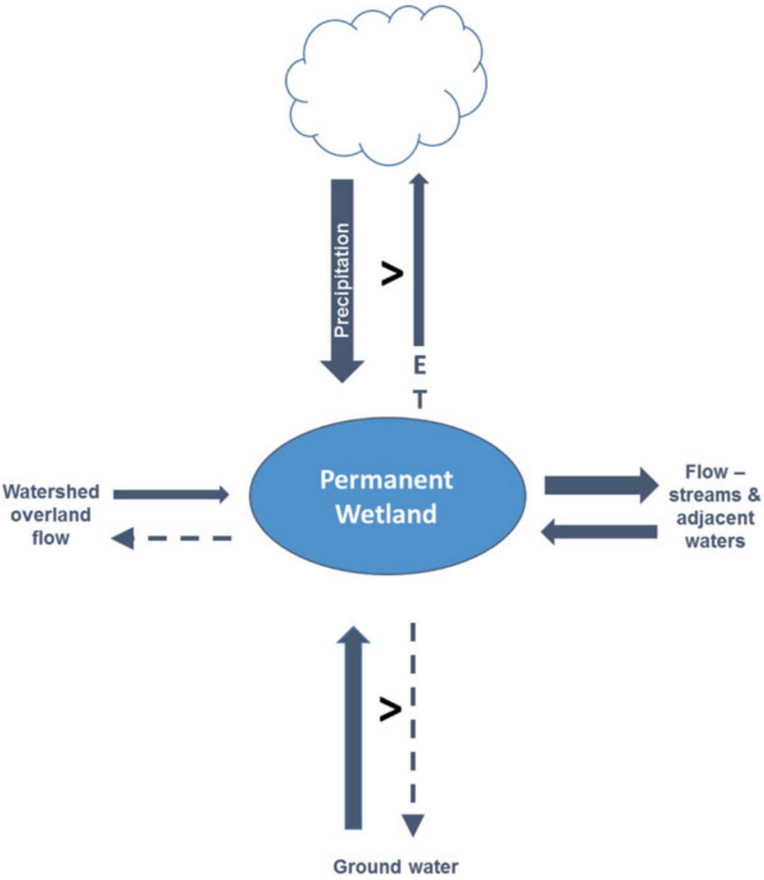

Fig. 8.1 Generalized factors responsible for water movements in permanent wetlands. *Arrow* weights depict relative magnitude of water exchange by individual pathways. *Dashed arrows* indicate relationships of minor importance, but these are often poorly known

charge in shallow waters throughout the region (Winter and Rosenberry 1995). Across the central portion of this area, many small waters were originally isolated and surface connectivity had been a relatively minor factor in water exchange, but this seems to be changing with increasing anthropogenic activity (wetland draining, ditching) and extreme precipitation cycles (Hanson et al. 2005; Herwig et al. 2010).

Vast numbers of permanent wetlands in other regions of the United States and Canada are also of glacial origin. Permanent wetlands are widespread throughout western boreal portions of north-central Alberta, Canada (Bayley et al. 2013). Here, poorly drained outwash plains, moraines, and flat lacustrine plains are prevalent, with wetland water chemistry influenced by relatively thick underlying peat layers in some areas (Bayley et al. 2013). Abundant sediment organic matter and adjacent peatlands contribute to low alkalinity, high levels of total phosphorus (TP) and phytoplankton biomass, and high productivity which often support well-developed communities of plankton and submerged aquatic vegetation (SAV) (Bayley and Prather 2003; Bayley et al. 2013).

Some of the most-studied permanent wetlands (or shallow lakes) in the world are those within lake districts of the northern and western Netherlands and the Norfolk Broads of the United Kingdom. Many of these waters formed following peatland excavations during the seventeenth century (Gulati and Van Donk 2002). Other waters are the result of centuries-old networks of dykes and dams which impounded inland waterways and produced permanent wetlands (or "broads," Moss et al. 1996). Subsequently these wetlands became important habitat for fish production and recreational use, and sometimes supplied water for irrigation of agricultural fields. Prior to the mid-twentieth century, many of these shallow waters exhibited oligotrophic conditions with low nutrient levels, clear water, and lush communities of SAV. With increasing external nutrient loading, many sites transitioned to turbid conditions with poor water quality, further resulting in loss of SAV, declining habitat for piscivorous fish, and diminished recreational value.

Permanent wetlands also occur widely in Mediterranean climates. On the Iberian peninsula in central Spain, permanent wetlands are common. Cladoceran zooplankton communities, especially *Daphnia* spp., have been the focus of studies in these waters due to concerns about lake responses to agricultural chemicals and encroachment, nutrient loading, introduction of non-indigenous fish stocks, and possible effects of climate change (Romo et al. 2004; Fernández-Aláez et al. 2004). Most natural lakes in Greece are shallow waters <1000 ha in size and would be considered permanent freshwater wetlands in our context. These waters have become increasingly valued for recreation and wildlife values, but are threatened by dramatic water-level reductions, eutrophication, and chemical contamination (Coops et al. 2003).

Lake Apopka is a subtropical freshwater wetland in Florida (United States), covering 124 km^2 and averaging 1.7 m depths (Carrick et al. 1993). This wetland overlies clastic, calcareous soils and is characterized by high alkalinity, extreme wind-induced turbidity, and poorly consolidated muck-like sediments. Due to low water clarity, sparse SAV, and declining fish populations, the site has been the subject of one of the most costly rehabilitation efforts in North America (Scheffer 2004). Tropical and subtropical permanent wetlands are well known from South America and Africa. Kosten et al. (2012) surveyed water quality parameters in 83 wetlands along the eastern coast of South America. These waters had a mean depth of 1.9 m, but varied widely in surface area from 0.6 to 27,000 ha. Lake Naivasha near Nairobi, Kenya is a premier destination for bird watching, but its ecological health has declined dramatically due to surrounding urbanization and agriculture, nutrient loading, altered hydrology, and introduction of non-indigenous fish, rusty crayfish (*Procambarus clarkia*), and other invasive species (Harper and Mavuti 2004).

Permanent wetlands are sometimes large and can be prominent landscape features. For example, Lake Arresø is the largest waterbody in Denmark (approximately 40 km^2) and has an average depth of only 3 m. Lake Taihu, the third largest waterbody in China, consists of a vast shallow basin (surface area of 2338 km^2, mean depth = 1.9 m) with extensive submerged, emergent, and floating-leaf vegetation and associated marshlands (Qin et al. 2007). Forty million people live within this lake's watershed (Qin et al. 2010), and the lake provides numerous economic, recreational, and transportation benefits.

Despite extreme variability in formation processes, geomorphology, and hydrology, it is possible to characterize some key features of these habitats, many of which affect aquatic invertebrate communities. These waters are permanently flooded yet shallow enough to permit polymixis throughout open-water periods, and usually allow considerable light penetration to substrates over large areas. Permanent flooding and well-lighted substrates allow for extensive development of emergent and submergent vascular plant communities over a majority of the basin. Thus, permanent wetlands are characterized by a high intensity of physical processes and biological interactions, and biological, chemical, and physical aspects are profoundly affected by complex influences of polymixis, high light availability, and shallow water columns. Organisms (including aquatic invertebrates) often coexist in close proximity with one another and food-web interactions along with water-sediment exchanges are particularly intense (Jeppesen et al. 1997). Physical properties such as light, wind-induced resuspension of sediments, and internal nutrient loading often play larger roles here than in deeper counterparts (Scheffer 2004). As will be elaborated later, permanent wetlands also have a propensity to exhibit alternative stable equilibria (Moss et al. 1996; Romo et al. 2004; Fernández-Aláez et al. 2004; Scheffer 2004; Zimmer et al. 2009). One stable state has low water transparency and sparse SAV (turbid state) while the other has clear water and abundant SAV (clear state). Among freshwaters, permanent wetlands are uniquely affected by this propensity for transitions between clear- and turbid-water states, and aquatic invertebrates both influence, and respond to, these ecological dynamics (Fig. 8.2).

Aquatic Invertebrate Taxa of Permanent Wetlands

The appendix provides a list of the families of aquatic invertebrates reported from a variety of permanent wetland and shallow lake habitats. Permanent wetlands that are covered by other chapters in this book (e.g., lakeshore or riverine marshes, temperate and tropical floodplain wetlands, beaver ponds, Everglades) were not included in this Appendix. Also excluded were taxa from study site descriptions lacking sufficient information to properly define the habitat, or taxa lists that did not distinguish among habitats when several types were sampled. Where more than one habitat type was surveyed (e.g., temporary and permanent wetlands), only

Fig. 8.2 Permanent wetlands exhibit two alternative stable states in many parts of the world. One state is the clear-water condition dominated by submerged aquatic macrophytes with low phytoplankton abundance (background above), and the other state a turbid-water condition dominated by phytoplankton with low abundance of submerged aquatic plants (foreground above). Aquatic invertebrates play a key role in stabilizing both states, and also in inducing shifts from one state to the other. Photo by Brian Herwig (used with permission)

those invertebrates identified as coming from the permanent habitats were included in our list.

A total of 176 families have been reported from permanent wetlands around the world, based on the 27 publications used to assemble our list. Of this number, 75 families were reported from only one continent, with North America and Australia having the largest number of restricted families at 21 each. Only two macroinvertebrate families, Chironomidae and Coenagrionidae, and three microcrustacean families, Cyclopidae, Daphniidae, and Chydoridae, were ubiquitous.

Key Factors Controlling Invertebrates in Permanent Wetlands

Hydrology Controls

In non-permanent wetlands, hydroperiod, along with underlying hydrology, is usually the most fundamental determinant of invertebrate community structure (e.g., how does shortening the inundation period of seasonal wetlands influence invertebrate communities?). In contrast, constant inundation, often with only nominal water-level fluctuations in a single growing season, is typical for many permanent wetlands, where standing water usually persists year-round. In permanent wetlands, research on hydrology and invertebrates has focused on a suite of factors that become more important with extended inundation. Along a hydroperiod continuum, abiotic factors (e.g., desiccation) are most influential in non-permanent wetlands, while biotic interactions (e.g., predation, competition) become increasingly important in permanent wetlands (Wellborn et al. 1996). The roles of predation and other biotic factors have emerged as key proximate drivers, contributing to the high variability often observed among permanent wetlands, even within a given geographical region such as the PPR in North America (Hanson et al. 2005; Anteau et al. 2011). Fish predation is one of the most important determinants of invertebrate community structure in permanent wetlands, and fish presence/absence and community composition are influenced by wetland depth, overland flooding, and connectivity to other waterbodies. Thus, wetland and watershed hydrology have strong indirect influences on invertebrate communities in permanent wetlands via influences on fish distribution and abundance.

At the same time, certain abiotic factors, influenced by hydrology, remain important in permanent wetlands. For example, interactions among underlying soils and geology, ground water, and climate can result in permanent wetlands that range from fresh to saline (Kantrud et al. 1989). Salinity can impact the aquatic invertebrate community indirectly through impacts on aquatic plants (Lacoul and Freedman 2006) or through direct osmoregulatory toxicity (Bayly 1972). Salinity tolerance varies among aquatic invertebrates. Hammer et al. (1990) noted that species richness of macroinvertebrates decreased rapidly at salinities greater than 15 ‰. Pinder et al. (2004) found salinity to be the primary influence on the distribution of aquatic invertebrates in wetlands of the wheat belt region in Western Australia.

Interactions with Plants and Algae

In wetlands with greater depths and relatively stable water levels, aquatic macrophytes with emergent and submersed growth forms become prominent features and critical habitat for many types of aquatic invertebrates. Aquatic plants increase surface area and habitat complexity, providing additional living space and food within the water column (Cyr and Downing 1988). Both diversity and abundance of aquatic macrophytes increase macroinvertebrate taxon richness and abundance (Zimmer et al. 2000; Hassall et al. 2011), and invertebrate communities often vary among different plant species or communities (Bazzanti et al. 2008). Aquatic plants serve as sites for oviposition, emergence, pupation, attachment, respiration, and as building materials and food (reviewed by Newman 1991). Moreover, presence of aquatic macrophytes contributes to changes in the physical and chemical environment of wetlands, and modifies influences of predator–prey interactions (Carpenter and Lodge 1986).

Given the strong relationship between aquatic plants and invertebrates, grazing of aquatic plants by vertebrate herbivores can indirectly influence invertebrate communities. Muskrats (*Ondatra zibethicus*) are important herbivores in permanent wetlands and shallow lakes (Fritzell 1989). Through their consumption of emergent macrophytes, and harvest of plant material for use in the construction of lodges, muskrats dramatically modify wetland habitats. Such activities have been found to alter abiotic conditions and wetland invertebrate communities (de Szalay and Cassidy 2001). Similar effects have been found for waterfowl that graze submersed macrophytes. Wrubleski (1989) observed contrasting Chironomidae communities in areas where waterfowl had consumed the submersed aquatic macrophytes relative to areas where the plants were protected from grazing.

Research has historically focused on the influence of macrophytes on aquatic invertebrates. However, recent work has shown that invertebrates may conversely also affect submerged macrophytes, indirectly, by controlling abundance of phytoplankton and epiphyton (Scheffer 2004). Epiphyton (and other types of periphyton) and phytoplankton are readily consumed by aquatic invertebrates, and high invertebrate grazing rates can reduce the abundance of both phytoplankton (Hanson and Butler 1994b) and periphyton (Jones and Sayer 2003). Alternatively, low grazing rates of invertebrates can permit periphyton and phytoplankton to accumulate, and resulting light limitation can reduce macrophyte abundance (Sand-Jensen and Borum 1991). Reduced macrophyte abundance, in turn, feeds back to the invertebrate community as described above. Thus, interactions among aquatic invertebrates, epiphyton, phytoplankton, and submersed macrophytes become very complex in permanent wetlands, and play key roles in generating alternative stable states (as elaborated below).

Investigators have also explored the functional importance of invertebrates in processing detritus in wetland food webs, helping to clarify relationships among organic matter, litter decomposition, nutrient cycling, and functional feeding groups of invertebrates in freshwater marshes (Wissinger 1999; Murkin and Ross 2000). Some of this research suggests that macroinvertebrates may play relatively minor roles in nutrient processing (Murkin and Ross 2000), but other studies indicate that zooplankton and macroinvertebrates have potential to translocate sediment-bound nutrients to overlying waters (Fukuhara and Sakamoto 1987), or to excrete nutrients directly to the water column (Vanni 2002).

Interactions with Predators

Fish Predation

Permanent hydroperiods greatly increase the likelihood that wetlands will sustain fish populations, although many remain fishless. The transition from fishless to fish presence represents one of the largest changes in invertebrate community structure in permanent wetlands. Planktivorous and benthivorous fish reduce community-scale biomass, production, and taxon richness of aquatic invertebrates (Batzer 1998; Zimmer et al. 2001b), and also have negative influences on individual taxa via predation or other indirect effects (Zimmer et al. 2000; Hanson et al. 2005). Fish also alter invertebrate behavior, including foraging activity (Johnson 1991), diel migration patterns (Burks et al. 2001), and patterns of oviposition (e.g., females detect chemical cues from fish and avoid laying eggs in basins with fish) (McPeek 1990a; Åbjörnsson et al. 2002). Planktivorous and benthivorous fish also influence invertebrate communities indirectly by favoring shifts to turbid-water states with low abundance of submerged macrophytes and high abundance of phytoplankton.

The importance of fish as a driver of invertebrate community structure in permanent wetlands is supported by both comparative field studies and controlled experiments. For example, Zimmer et al. (2002) compared natural fishless wetlands to wetlands with fathead minnows (*Pimephales promelas*), and found that large-bodied cladocerans and aquatic insects were up to 41-fold and fourfold more abundant in fishless sites, respectively, compared to sites with fish. Hanson and Riggs (1995) also compared invertebrate communities in Minnesota wetlands with and without fathead minnows and reported that invertebrate taxon richness, along with abundance and biomass of aquatic insects and crustaceans, were reduced in the presence of fish. Using experimental mesocosms, Åbjörnsson et al. (2002) reported that presence of fish reduced both biomass and species diversity of aquatic insects, but argued that diversity of large predatory insects may be lower in wetlands with fish because some free-flying insects detect and avoid waters with fish. At the community scale, Zimmer et al. (2000) used a multivariate approach and found that 19 invertebrate taxa (out of 32) occurred more frequently and in higher abundance in fishless wetlands, while only one family (Corixidae) was more abundant in wetlands with fish. Changes in invertebrate behavior between wetlands with and without fish have also been documented in several diverse taxa, with behaviors often focused on minimizing risk of predation by fish. For example, in the absence of fish, damselflies are active, mobile predators, but switch to lie and wait foraging to reduce their predation risk when fish are present (Johnson 1991). *Daphnia* detect chemical cues when fish are present, and undergo diel horizontal migration, moving to macrophyte beds during the day to reduce predation risks, then migrating back to open water at night when the risk of predation is lower (Burks et al. 2001). Several studies have shown that fish effects can exceed influences of abiotic factors (Tangen et al. 2003; Hanson et al. 2012).

Most studies of factors controlling wetland invertebrates have focused on relatively few variables (which is often necessary for large-scale research efforts). However, this limits interpretation and application of results because influences of many factors remain unaccounted for, some of which may be more important than variables included in simple models (Hanson et al. 2012). Relatively little research has assessed concurrent influences of a wide range of factors on wetland invertebrate communities, but available data shed some light on the relative magnitudes of biotic and abiotic influences. For example, Tangen et al. (2003) tested for relationships between land use and invertebrate community structure, but failed to find strong associations. Instead, fish presence/absence showed the strongest relationship to aquatic invertebrate communities. Similarly, Hanson et al. (2012) assessed relationships between invertebrate abundance and several watershed-scale and within-lake variables, and found that characteristics of the fish community were stronger predictors of invertebrate abundance than any measured variable at the watershed scale. Moreover, they also reported that invertebrate abundance was influenced more by simple fish presence/absence than by summed biomass of planktivores and benthivores, suggesting invertebrate communities exhibited a stronger categorical response to fish presence than to density-dependent predation. Further, Hanson et al. (2015) measured community correspondence to relate aquatic invertebrates to a broad suite of environmental variables measured in 104 permanent wetlands within the prairie, parkland, and forested regions of Minnesota. Results indicated that, after controlling for variability attributable to fish abundance, other biotic and abiotic variables were poor predictors of the remaining variation in zooplankton and macroinvertebrates. Overall, available data indicates that permanent wetlands with and without fish are very different ecologically, and that fish presence itself represents a major source of variability in abundance, species composition, and behavior of aquatic invertebrates in permanent wetlands.

It’s worth emphasizing that presence of fish in wetlands is naturally variable both temporally and spatially. Many studies emphasize impacts of fish using fish-enclosure experiments in single waterbodies, but this approach may have little relevance to natural fish-bearing systems where fish presence doesn’t vary so dramatically. In contrast, studies assessing direct and indirect influences of fish presence–absence on invertebrates across multiple permanent wetlands probably have more ecological relevance because results better mimic natural ecological responses to spatial and temporal variability in communities among these ecosystems (Zimmer et al. 2001a).

We believe there are several major reasons why fish have such strong ecological influences on aquatic invertebrate communities in permanent wetlands. First, in both spatial and temporal contexts, fish presence in permanent wetlands functions as a dynamic categorical variable, with some basins fishless, others with high densities of fish, and still other waterbodies switching from fish to fishless due to colonization or extinction events such as winterkill (Zimmer et al. 2001a; Herwig et al. 2010). Attributes of wetlands and their fish communities may also cause higher fish predation pressure on invertebrates compared to other lentic systems (i.e., deeper lakes). Jeppesen et al. (1997) argued that top-down effects of fish on invertebrates are particularly strong in permanent wetlands because, compared to other systems, (1) fish biomass per unit volume of water is higher, (2) piscivores represent a smaller proportion of the fish community, (3) benthic invertebrate abundance is higher and more accessible to fish, so fish predators rely less on zooplankton prey, and (4) vertical migration of invertebrates to deeper refuge areas is not possible.

Broad diets and high consumption rates also contribute to strong influences of fish on invertebrates in permanent wetlands. Analysis of diets from fish in permanent wetlands confirms that fish consume a wide spectrum of invertebrates, ranging in body size from rotifers to Odonata, and constituting all functional feeding groups (Herwig and Zimmer 2007; Verant et al. 2007). Even fish typically considered piscivorous, such as walleye (*Sander vitreus*), consume numerous invertebrates in permanent wetlands (Ward et al. 2008). The wide spectrum of diet often causes fish predation to have nearly community-wide suppression of invertebrate abundance (Zimmer et al. 2000). Moreover, consumption rates of invertebrates by fish can be very high. Several studies have used bioenergetics modeling to estimate consumption rates of invertebrates by fish, and have found that consumption rates approximate or even exceed production rates of invertebrates during the peak growing season (Duffy 1998; Herwig and Zimmer 2007).

Fish predation on invertebrates is also intensified in permanent wetlands because many invertivorous fish species are not themselves vulnerable to predation by piscivores. In wetlands, benthivorous taxa often outgrow the threat of predation by gape-limited piscivores, and many benthivorous and planktivorous fishes have spines and barbs that defend against predation (e.g., yellow perch *Perca flavescens*). The net result is piscivores are unable to reduce the abundance of invertivores in diverse fish communities, and invertebrate abundance in those wetlands remains low even in presence of piscivores (Friederichs et al. 2011). Finally, fish can influence invertebrate communities indirectly by inducing major changes in abundance of primary producers (Zimmer et al. 2009). High densities of planktivorous and benthivorous fish tend to favor shifts to turbid states with low abundance of submerged macrophytes, which has major impacts on many aquatic invertebrates by changing habitat complexity and the dominance of primary producers (Scheffer 2004).

While many studies from permanent wetlands have reported that fish reduce invertebrate abundance across a variety of taxa, trophic relationships are complex and several studies have reported some apparently contradictory relationships. For example, McParland and Paszkowski (2006) found that gastropods decreased following introduction of fish, while abundance of amphipods and chironomids increased. These authors hypothesized that amphipods and chironomids increased because fish reduced the abundance of their gastropod competitors. Batzer et al. (2000) reported similar results, where fish reduced the abundance of competitors and predators of midge larvae, resulting in a positive overall effect of fish on midge abundance. Moreover, several studies in the PPR of North America have found positive relationships between presence of fish and abundance of Corixidae (Zimmer et al. 2000; Tangen et al. 2003). The mechanisms for this relationship are unknown, but Corixidae may be less sensitive to fish predation, or may benefit from reduced competition when other invertebrates are suppressed by fish. Batzer (1998) suggested that the importance of fish predation on benthic midges varied seasonally, with minimal influences in early summer but more pronounced effects evident during mid-late season. It is perplexing why some studies have found positive effects of fish on select taxa, while others have found consistent negative effects across nearly all taxa. However, variation in fish abundance, the taxonomic composition of fish communities, habitat complexity, and methodological approaches probably all contribute to the range of findings.

Other Predators

Besides fish, other predatory vertebrates may also have important influences on invertebrates, via both direct and indirect effects, especially in fishless habitats. In northern PPR wetlands, gray tiger salamanders (*Ambystoma mavortium diaboli)* can be very abundant, reaching densities of 5000 ha^{-1} (Deutschman and Peterka 1988). These salamanders consume a variety of invertebrates, particularly larger prey such as amphipods and chironomids (Olenick and Gee 1981). Benoy (2008) reported that as tiger salamander abundance increased across 45 PPR wetlands, aquatic insect abundance declined and phytoplankton standing crop increased. These results support the idea that tiger salamanders mimicked the effect of planktivorous fish, inducing cascading effects on the trophic structure of prairie potholes.

In the absence of fish or other vertebrate predators, large-bodied invertebrate taxa such as Odonata, Dytiscidae, and Notonectidae function as top predators (reviewed by Batzer and Wissinger 1996). Many studies have documented the importance of invertebrate predation on invertebrate prey in littoral-type habitats (McPeek 1990b; Åbjörnsson et al. 2002), and invertebrate predators such as *Chaoborus* also have a strong influence on zooplankton communities in fishless water columns (Arnott and Vanni 1993). Similar to fish, invertebrate predators in fishless habitats influence community assemblages (McPeek 1990b), abundances of individual taxa (Åbjörnsson et al. 2002), and the outcomes of competitive interactions (Blois-Heulin et al. 1990).

Invertebrate predators consume not only other invertebrates, but they sometimes alter the presence or behavior of vertebrates. For example, gray treefrog (*Hyla chrysoscelis*) tadpoles reared with predatory dragonfly (*Aeshna umbrosa*) larvae differ in shape and color from tadpoles reared in the absence of dragonflies (McCollum and Leimberger 1997). Smith (1983) reported that in permanent forest pools, dragonfly larvae (*Anax junius*) eliminated chorus frog tadpoles (*Pseudacris triseriata*) when they occurred together in the same pool. While most research on predation in freshwaters has focused on clarifying patterns in response to fish, work to date shows that invertebrate predators likely have important roles structuring invertebrate communities in permanent wetlands, and elucidating those role merits much more study.

A Conceptual Framework for Invertebrate Communities in Permanent Wetlands: Hydrogeomorphology and Alternative Stable States

Permanent wetlands worldwide have been shown to exist in two or more alternative stable states, with the two most common states comprised of a phytoplankton dominated, turbid-water state, versus a submerged macrophyte-dominated, clear-water state (Scheffer 2004) (Fig. 8.2). Both states are relatively stable, although wetlands can shift back and forth between these contrasting conditions (Scheffer et al. 1993). Aquatic invertebrates have been shown to be important for both stabilizing the clear-water state and for inducing shifts between states (Hanson and Butler 1994b; Jones and Sayer 2003). Because of the strong influence of fish on aquatic invertebrates, the importance of invertebrates for stabilizing the clear-water state, and the management emphasis on maintaining clear water (Scheffer et al. 2006), recent research on aquatic invertebrates in permanent wetlands has been focused on understanding the complex relationships among fish, aquatic invertebrates, and alternative stable states at the ecosystem scale.

Aquatic invertebrates stabilize the clear-water state in permanent wetlands two ways. First, zooplankton like *Daphnia* maintain low phytoplankton abundance in spring and early summer while aquatic macrophyte and epiphyton biomass is relatively low (Scheffer 2004). Grazing rates of zooplankton can be very high. For example, Hanson and Butler (1994a) estimated filtration rates of 100–200 % in a large permanent wetland (Lake Christina, MN) following a fish die off. Resulting spring "clear-water phases" may be short-lived, but elevated light levels to wetland sediments are often none-the-less sufficient to trigger growth of submerged macrophytes and epiphyton. This new growth (especially epiphyton) sequesters nutrients from the water column which then helps maintain low phytoplankton abundance for the remainder of the growing season (Scheffer 2004). However, low densities of zooplankton can also induce shifts from clear to turbid states. For example, if densities of planktivorous fish are high during early spring, abundance of zooplankton may be too low to control phytoplankton abundance, leading to high turbidity with low macrophyte abundance, shifting a wetland to the turbid state. Wetlands usually remain in a turbid condition until abundance of planktivorous fish declines to levels low enough to allow zooplankton to again reduce phytoplankton abundance, facilitating a shift back to the clear-water condition (reviewed by Scheffer 2004). As in deeper systems, high densities of planktivorous fish in permanent wetlands induce size-selective predation on zooplankton, resulting in a shift from large-bodied forms like *Daphnia* to small-bodied forms like *Bosmina* (Hanson and Butler 1994a). Although densities of the small-bodied zooplankton can be relatively high, their capacity to control phytoplankton is far lower than large-bodied forms (Lynch and Shapiro 1981) and phytoplankton abundance remains high. Also, if wetlands are sufficiently shallow, submerged macrophytes may persist even in turbid-state conditions because short water columns allow some light penetration to plants growing near the sediment surface.

A second way aquatic invertebrates stabilize clear-water states in wetlands is by exerting sufficient grazing pressure on epiphyton, essentially increasing survival and growth rates of submerged macrophytes by reducing the shading otherwise due to an overgrowth of surface-associated algae. Here the key invertebrates are littoral and benthic forms, especially epiphyton grazers such as gastropods and Ephemeroptera. Jones and Sayer (2003) showed that at high densities invertebrate grazers have potential to reduce epiphyton and prevent shading out of submerged plants. However, sufficiently high densities of insectivorous and molluscivorous fish can reduce epiphyton grazers, allowing epiphyton abundance to increase, favoring large-scale macrophyte declines and triggering transitions to turbid conditions (Jones and Sayer 2003). Thus, the clear-water state in temperate wetlands is stabilized by two different groups of invertebrates, with zooplankton grazing on phytoplankton important in spring and early summer, and littoral-benthic epiphyton grazing becoming more important through the rest of the growing season.

Aquatic invertebrates play a prominent role in inducing state shifts in many permanent wetlands, but other factors can also cause a shift from a clear to turbid state. Nutrient loading can decrease the stability of the clear-water state to the point that a shift occurs to the turbid state, and the turbid becomes the only stable state (Moss et al. 1996). Research has shown that fish are one of the best predictors of shifts to the turbid state, with increasing likelihood of turbid lakes with elevated biomass of planktivorous and benthivorous fish (Zimmer et al. 2009; Nolby et al. 2015). Fish can induce shifts to turbid states via predation effects on invertebrate grazers of phytoplankton and epiphyton, but they can also induce shifts by direct disturbance. Large-bodied benthivores like common carp (*Cyprinus carpio*) uproot submerged macrophytes (Crivelli 1983), and many benthivores may also increase turbidity by disturbing sediments with their feeding activities (Breukelaar et al. 1994), resulting in lower water transparency for submerged plants. Lastly, benthivorous fish may increase internal nutrient loading to the water column by disturbing sediments or by feeding on detritus and translocating nutrients to the water column via excretion (Zimmer et al. 2006). Overall, benthivorous and planktivorous fish favor shifts to the turbid-water state, with subsequent impacts on aquatic invertebrates. Thus, fish impact invertebrate communities both directly via predation and indirectly by favoring the turbid-water state.

Shifts to the turbid-water state influence aquatic invertebrates in multiple ways. First, primary production shifts from submerged macrophytes and epiphyton to phytoplankton and perhaps to sediment-associated algae growing in shallow water with sufficient light (Vadeboncoeur et al. 2003). This shift at the base of the food-web changes the competitive advantage among invertebrate grazers, shredders, and collectors to species benefitted by high abundance of phytoplankton (Hargeby et al. 1994). Loss of submerged macrophytes also reduces habitat complexity and predation refuge for invertebrates, resulting in increased vulnerability to fish predation (Crowder and Cooper 1982) and altered predator–prey relationships among the invertebrates (Burks et al. 2001).

Fish have strong influences on invertebrates, but not all permanent wetlands have fish, so understanding factors driving fish distributions is necessary for understanding variability in invertebrate communities. A permanent hydroperiod does not ensure a wetland basin will support fish and the status of fish populations in permanent wetlands is quite variable, both within and among wetlands. In the southern PPR of Minnesota, for example, approximately 93 % of permanent wetlands had fish populations (Herwig et al. 2010). On the Canadian side of the PPR, Lawler et al. (1974) found that only 10–20 % of wetlands in southwestern Manitoba supported fish. More recently, Anteau and Afton (2008) reported that 31–45 % of wetlands they sampled in central North Dakota contained fish and that fish populations occurred in 74–84 % of semipermanent and permanent wetlands they sampled in Minnesota and Iowa, along the southeastern margin of the Prairie Pothole Region (PPR) of central North America. These data are consistent with those of Hanson et al. (2005) who suggested that ecological influences of fish in permanent wetlands may increase along a northwest to southeast gradient in the PPR. Even in north-temperate permanent wetlands, fish communities can be surprisingly diverse. Herwig et al. (2010) sampled fish populations in >70 permanent wetlands in Minnesota and reported that 22 fish species occurred in more than one of these sites. They reported that fish species richness averaged 3–4, and that richness was positively correlated with wetland size and watershed area. Large permanent wetlands in North America and elsewhere support diverse, perennial fish populations and several fish feeding guilds (planktivores, benthivores, piscivores) sometimes occur in these systems (Herwig et al. 2010; Friederichs et al. 2011). Although our review indicates that summaries of fish population data from tropical wetlands are limited, fish assemblages in these waters can be much more diverse, especially given effects of repeated introduction of exotic fish species (Jeppesen et al. 2007). While status of fish populations in permanent wetlands is often unknown and probably fluctuates over time, this constitutes a critical ecological threshold that must be considered along with other factors structuring invertebrate communities.

What drives the variability in fish presence among permanent wetlands? At large scales, such as the contrast between the northwestern and southeastern portions of the PPR described above, differences are likely due to variability in climate and wetland morphometry (Hanson et al. 2005). At local scales, classic island biogeography principals appear to be important (Scheffer et al. 2006). Lack of surface-water connectivity and isolation decrease the likelihood that a wetland will be colonized by fish, while reduced wetland depth increases the probability of extinction for existing populations due to winterkill or other factors (Herwig et al. 2010; Nolby et al. 2015). Herwig et al. (2010) studied permanent wetlands along the eastern margin of the PPR in Minnesota and reported that all sites connected to potential sources of fish (e.g., streams and other permanent wetlands) supported fish, as did all unconnected basins with maximum depths greater than 2.15 m. In those wetlands, fish occurred in connected basins because these populations recolonized yearly even if they were eliminated by winterkill. Fish populations also occurred in isolated, but relatively deep basins. This probably reflects the fact that greater water depth reduces frequency (and extent) of winter hypoxia and winterkill, allowing fish populations to persist over long time periods. Fish populations in isolated, deep basins in the PPR may result from rare flooding events allowing periodic colonization in these permanent habitats.

Similar to deeper lakes (Hershey et al. 1999), landscape and wetland basin hydrogeomorphology (wetland depth, connectivity, etc.) appear to have indirect

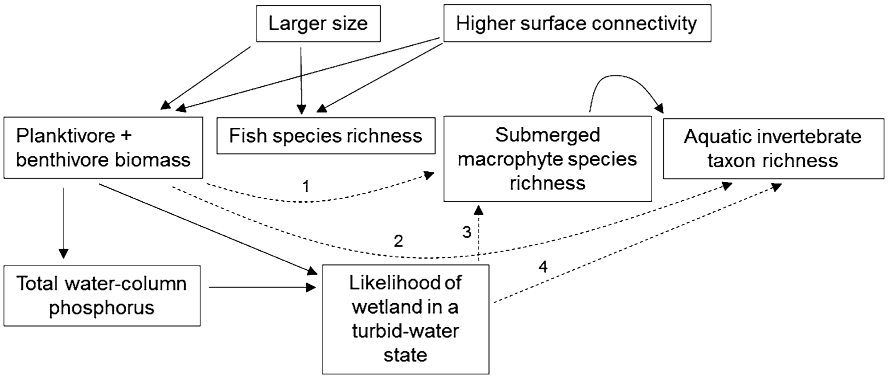

Fig. 8.3 Relationships influencing aquatic invertebrate biodiversity in permanent wetlands (based on Nolby et al. 2015). Solid lines indicate a positive relationship; dashed lines are negative relationships. Lake size and connectivity have a positive influence on planktivore+benthivore biomass. Planktivore+benthivore biomass have negative influence on biodiversity of macrophytes and invertebrates, while total phosphorus and planktivore+benthivore biomass favor turbid states which also has negative impacts on diversity of macrophytes and invertebrates. Although classic island biogeography predicts positive relationships among biodiversity, wetland size, and extent of surface connectivity, influences of planktivorous and benthivorous fish uncouple submerged macrophytes (1) and aquatic invertebrate communities (2) from positive effects of lake size and connectivity. Submerged macrophyte (3) and invertebrate (4) richness are also reduced following transitions to turbid-water states

effects on invertebrate communities in permanent wetlands via influences on fish distribution. Hydrogeomorphology is probably even more influential for invertebrates in wetlands relative to deeper lakes due to intense fish predation and the tendency of planktivorous and benthivorous fish to induce turbid-water states. In complex ways, hydroperiod, maximum depth, and surface connectivity all influence aquatic invertebrate community structure in permanent wetlands through physical processes, but also indirectly by interacting to determine spatial and temporal patterns of fish presence (Fig. 8.3).

Abundance, community composition, and behavior of aquatic invertebrates in permanent wetlands are controlled by a suite of factors that vary in importance from one basin to the next. However, our review suggests that abiotic factors always remain important. Salinity has direct influence on invertebrate communities, but also has indirect influences via limiting distribution of fish and other predators. Wetland depth, wetland connectivity, and nutrient levels are important, but may operate indirectly by influencing the likelihood a wetland will have fish populations, and whether a wetland will be in a turbid or clear-water state. The net result is that invertebrate communities in permanent wetlands are controlled by a series of complex interactions involving both abiotic and biotic variables (Fig. 8.4).

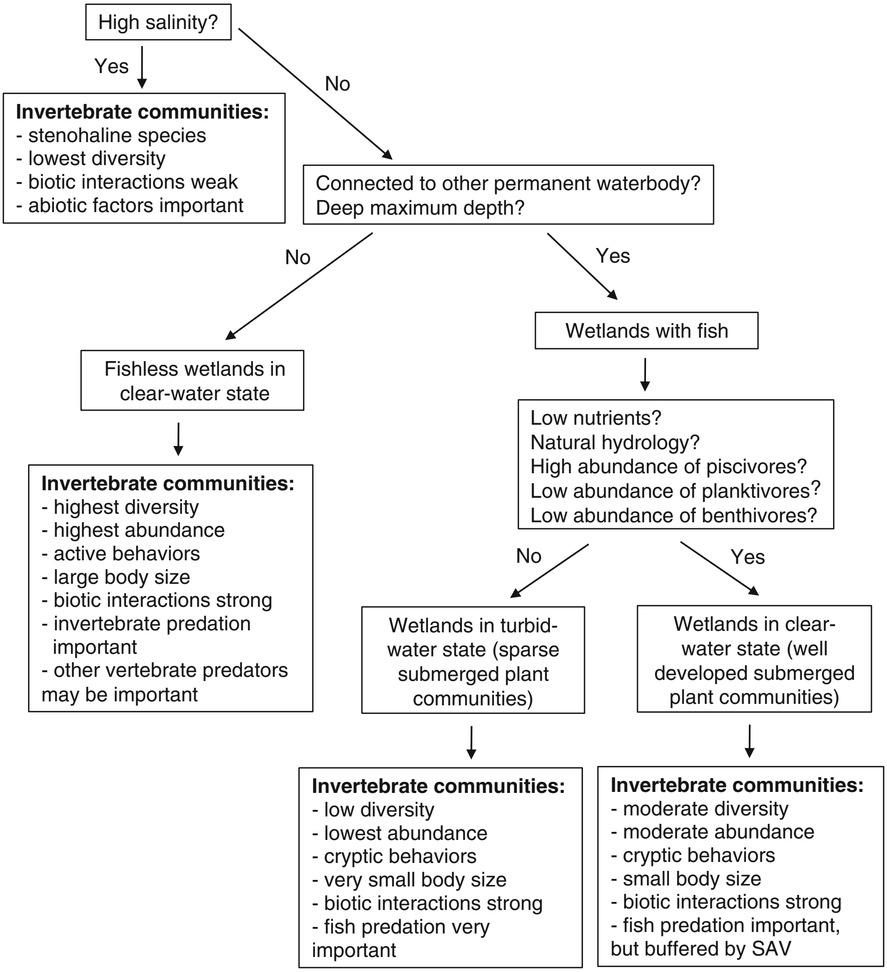

Fig. 8.4 Conceptual model summarizing broad relationships among fish, submerged macrophytes, aquatic invertebrates, and other characteristics of permanent wetlands

Management and Conservation Issues

Current Management and Conservation Issues

Research and management of aquatic invertebrates in permanent wetlands was historically directed toward wetland wildlife, and was mostly focused on understanding invertebrates in the context of their importance as food resources for wetland-dependent vertebrates. For both researchers and managers, we advocate a broader valuation of the roles of aquatic invertebrates in maintaining high water quality and healthy ecological communities in permanent wetlands and shallow lakes.

Perhaps the best conceptual framework illustrating the need for incorporating aquatic invertebrates in wetland management strategies comes from recent work showing the importance of invertebrate communities in the alternative stable state model. As described in detail above, understanding alternative states in permanent wetlands is key to understanding the basic ecology of those ecosystems, and invertebrates play key roles. Many of the conservation issues facing permanent wetlands are important because they influence the stability of alternative stable states and aquatic invertebrates and other wildlife are impacted as wetlands shift states. Management efforts in permanent wetlands often focus on maintaining the clear-water state due to its perceived higher value as habitat for wetland-dependent species (Hanson and Butler 1994a; Scheffer et al. 2006) and greater aesthetic appeal (Moss et al. 1996). Understanding the roles of aquatic invertebrates in controlling abundance of periphyton and phytoplankton, and appreciating the influences of fish on aquatic invertebrates, are key to anticipating whole-ecosystem changes as wetlands transition between clear- and turbid-water states. Studies of invertebrate communities in permanent wetlands identified primary drivers of invertebrate abundance, diversity, and community structure, but also clarified the importance of zooplankton, benthic, and littoral macroinvertebrates in promoting high water clarity and diverse macrophyte communities in the clear-water state. Along with better-known roles in food chain support for waterfowl and other wetland wildlife, this emerging understanding of ecological relationships among water quality, SAV, and alternative stable states points to the need for conservation of aquatic invertebrate communities to favor healthy macrophyte communities and clear-water states in permanent wetlands worldwide (Moss et al. 1996; Scheffer 2004; Zimmer et al. 2009).

Our experience and literature review indicates that several issues are among the most pressing for management of permanent wetlands. Importance of these factors was illustrated by historical research, but subsequent work has clarified the roles of invertebrates in the broader ecological dynamics and alternative ecosystem states of permanent wetlands. Recent efforts also underscore the need for attention to these issues in order to facilitate conservation of aquatic invertebrates and to preserve their functional roles in shallow waters.

First, introduction and proliferation of invasive (albeit sometimes native) fish populations is a critical conservation issue because they often threaten communities of wetland aquatic invertebrates in both north-temperate and tropical regions. The transition from fishless to fish-bearing in permanent wetlands induces a major reorganization of invertebrate behavior and community structure due to direct and indirect effects of predation (Wellborn et al. 1996) and this threshold has been shown to be important in permanent wetlands (Zimmer et al. 2000; Hanson et al. 2012). Both planktivorous and benthivorous fish favor shifts to the turbid state, with subsequent negative effects on most invertebrates due to reduced abundance of SAV (Zimmer et al. 2009; Nolby et al. 2015). Not surprisingly, shallow lake management efforts have traditionally included measures to limit or eliminate dense, undesirable fish populations. Strategies often involve the use of fish toxicants to remove as many fish as possible from deteriorated shallow waters (Hanson and Butler 1994a, b; Zimmer et al. 2001c). In some cases, piscivore stocking has also been used to limit populations of undesirable fish in North America and Europe (Potthoff et al. 2008). These efforts are costly and labor-intensive, but often produce dramatic short-term improvements in water quality and invertebrate communities (Hanson and Butler 1994b; Søndergaard et al. 2007). Unfortunately, target fish populations are rarely eradicated and can recover quickly (Duffy 1998). In our experience, improvements in permanent wetlands following fish removals rarely persist more than 5–10 years. Even when complete fish kills are achieved, migration corridors often allow fish to recolonize permanent wetlands within short periods (Zimmer et al. 2001a).

While management of fish has focused on population control via piscicides or limiting fish access via fish barriers on a basin-by-basin basis, we encourage managers to supplement these tactics with broader approaches where fish dispersion and colonization are addressed at a landscape scale. Installation of culverts and drainage tile, digging of ditches, and integration of wetlands and deeper basins across large spatial scales favors persistent populations of fish in wetlands (Hanson et al. 2005; Herwig et al. 2010). Additionally, increased connectivity also favors dispersal of invasive species among wetland basins, and several studies have documented the impacts of invasive species on invertebrate communities in permanent wetlands (Harper and Mavuti 2004; Rodríguez et al. 2005). Limiting these landscape modifications may help preserve natural variability in community composition among multiple wetland basins, potentially alleviating the need for intensive site-by-site management. Preserving fishless wetlands seems especially important for maintaining aquatic invertebrate diversity at a landscape scale, as many taxa are found more often and in higher abundance in fishless sites relative to those with fish (Wellborn et al. 1996; Nolby et al. 2015). Moreover, fishless wetlands may be uncommon in some parts of the world, and are likely threatened by surface connections to basins with fish. In the PPR of Minnesota (USA), for example, just 7 % of permanent wetlands are fishless, and during a 5-year study of 10 fishless wetlands, two were connected to basins with fish via ditching (Zimmer, personal observation).

The potential for competition between fish and waterfowl for invertebrate prey also highlights the importance of controlling unnatural fish distributions in permanent wetlands. Invertebrates have long been recognized as important prey for many species of waterfowl, especially for females during egg laying (Swanson and Duebbert 1989; Krapu and Reinecke 1992), and interest in waterfowl management stimulated many of the earlier studies on aquatic invertebrates in permanent marshes. Moreover, considerable diet overlaps between fish and many species of waterfowl-spurred-related work to clarify potential for resource competition for invertebrate prey. Early work identified the importance of a wide range of aquatic invertebrates as food for breeding waterfowl and other aquatic birds (Swanson and Duebbert 1989; Krapu and Reinecke 1992). Aquatic insects, crustaceans, snails, and other invertebrates were clearly shown to be required seasonally by breeding waterfowl foraging in temporary or seasonally flooded wetlands. Authors also acknowledged that permanently flooded wetlands were important, especially during drought, when small wetlands are unavailable (Swanson and Duebbert 1989), or as foraging areas for some species like canvasbacks and lesser scaup in North America (Hanson and Butler 1994b). Thus, fish management may be an important component for optimizing waterfowl habitat, especially in areas with limited numbers of temporary and seasonal wetlands.

A second major conservation need is maintenance of natural water-level fluctuations and hydroperiods (duration). Because communities here are comprised of both "wetland" and "lake" species, it might appear that conservation of natural hydroperiods is less critical for these areas; we reject that notion. In North America, altered hydrology usually results in increased maximum depths, stabilized water levels, and in some cases, longer hydroperiods, with permanent flooding of many areas that previously held water only seasonally. Marsh ecologists have shown that vegetation in shallow fresh waters is strongly influenced by flooding depth, frequency, and duration (van der Valk and Davis 1978). Water-level fluctuations, and especially increased water depth, influence virtually all aquatic vascular plants in freshwater wetlands including emergent and submergent forms (van der Valk 2005). Given these relationships, it is not surprising that hydrologic alterations affect vascular plant communities, nutrient cycling, and other properties in permanent wetlands and that natural water-level fluctuations are essential for maintaining wetland processes and biotic communities (Chow-Fraser 2005). Research has shown that permanent wetlands with natural hydroperiods show more diverse plant and animal communities than those with modifications to maintain more stable water levels (van der Valk 2005). Beyond direct implications for aquatic vascular plants, increases in depth and hydroperiod have other interrelated consequences including increased permanence for aquatic organisms (including fish), lower light levels at the sediment surface and ultimately conditions that favor transitions to turbid states (Scheffer 2004). Sustained high-water levels are almost certain to favor loss of SAV and may induce transitions to turbid states, at least in lakes with highly productive populations of benthivorous and/or planktivorous fishes (Coops et al. 2003; Hobbs et al. 2012). Similar to fish distributions, hydroperiod management must be addressed using landscape-level approaches to counter negative consequences of ditching, culvert installation, and consolidation of wetland basins outside an individual wetland's immediate watershed. Despite jurisdictional impediments to wetland drainage and changes to natural water regimes, these practices continue to be widespread throughout North America and elsewhere. Permanent wetlands have been drained less frequently than shallower basins with shorter hydroperiods due to logistical and legal impediments (Oslund et al. 2010), but modifications and even losses still occur in North America and loss rates are much higher in many other parts of the world (Dahl 2014).

Finally, invertebrate communities in many permanent wetlands around the world face severe threats from eutrophication and nutrient loading which affect aquatic invertebrate communities several ways. Higher nutrient levels increase abundance of inedible cyanobacteria (Kosten et al. 2012), favor winter hypoxia in lakes subject to ice cover (Meding and Jackson 2003), and reduce abundance of submerged macrophytes which increases potential for shifts to the turbid state. Nutrients have long been recognized as a primary driver of the stability of alternative states in permanent wetlands, with resilience of turbid states positively related to nutrient levels (Scheffer 2004). Moreover, at higher nutrient levels, greater reductions in fish biomass are needed to induce shifts to clear-water states (Gorman et al. 2014), making management of many turbid waters far more difficult. High external loading of nutrient levels can also have a “legacy” effect on permanent wetlands, where nutrient levels in the water column remain high and the turbid state remains stable long after external loading is reduced due to internal loading of nutrients from wetland sediments (Hobbs et al. 2012). Given the importance of nutrients for inducing transitions to turbid states and the prevalence of internal nutrient loading in permanent wetlands, managers should make control of eutrophication a top priority for conservation of aquatic invertebrates.

Eutrophication seems to be an even greater problem for permanent wetlands at lower latitudes because macrophyte abundance appears to decline at lower levels of nutrients compared to higher latitude wetlands (Kosten et al. 2009). It is important to recognize that trophic relationships among nutrients, water quality, aquatic invertebrates, and macrophytes are more variable and poorly known for tropical wetlands than for north-temperate sites. For example, Bachmann et al. (2002) reported no associations between water column nutrient levels and macrophyte abundance at all but the highest nutrient levels when macrophytes declined and phytoplankton became predominant in permanent wetlands in Florida. Broadly, we think tropical wetland resources need urgent attention from researchers and managers because ecological relationships are poorly known, and because exotic species, eutrophication, demographics, and economics are contributing to extreme pressure on these shallow permanent waters (e.g., Harper and Mavuti 2004). Managing external loading remains paramount yet is difficult due to the ubiquitous use of fertilizers in and around aquatic areas in many regions of the world, and due to the fact that nutrient reduction is a watershed-level issue that often involves multiple stakeholders with conflicting priorities.

Emerging Issues and Information Needs

Several other factors appear to be emerging conservation issues; research to date points to needs for management, yet these issues have received less study than those discussed above. Chemical pollution, defined broadly as pesticides, herbicides, heavy metals, and endocrine disrupting compounds, is an emerging concern for waters at the global scale, yet effects are poorly quantified (Rockström et al. 2009). The same is true for chemical pollution in permanent wetlands, along with impacts on invertebrate communities. Mesocosm and microcosm research have documented the potential toxicity of several commonly used pesticides on aquatic invertebrates found in permanent wetlands (Johnson 1986), and have shown that herbicides may alter relative abundance of primary producers and favor shifts to turbid states in wetlands (Vera et al. 2010). Additionally, researchers have documented pesticide levels in wetlands that exceed thresholds set for maintaining aquatic life by government agencies (Donald et al. 1999). New agricultural chemicals are being developed and those with high efficacy soon are used widely. Pesticides might be especially harmful to wetland invertebrates because applications often occur in close proximity to aquatic habitats, and many target arthropods. Main et al. (2014) recently reported that neonicotinoids are widely used in production of canola, corn, and soybeans across Canada's portion of the PPR. Transport of neonicotinoids into wetlands is likely, where the chemicals may persist for many months. Extensive application of this chemical is relatively new across the North-American prairies, but elsewhere data indicate that toxicity for aquatic invertebrates may be high, especially with prolonged exposure (Main et al. 2014). Additional work on occurrence rates and concentrations of pesticides in wetlands in agricultural areas is clearly needed (Goldsborough and Crumpton 1998).

Research is also needed to clarify the influences of invasive species on wetland invertebrates. Invasive species are known to be a major threat to biodiversity, perhaps second only to habitat destruction (Simberloff et al. 2005), and wetlands are especially prone to colonization by invasive species due to their function as landscape "sinks" (Zedler and Kercher 2004). Information about invasive species effects on aquatic invertebrates in permanent wetlands is relatively scarce, but available evidence suggests the impacts can be large. For example, introduced crayfish in Lake Naivasha, Kenya, reduced macrophyte biomass with impacts cascading to the native invertebrate communities (Harper and Mavuti 2004). More broadly, loss of submerged plant biomass due to invasive species has been shown to induce shifts to turbid states in wetlands, with subsequent impacts on aquatic invertebrates and other organisms (Rodríguez et al. 2005). Threats to conservation of wetland invertebrates from invasive species seem likely to accelerate with an increasingly global society and as urbanization encroaches on remaining permanent wetlands. Urbanization itself also appears to be an emerging threat to conservation of aquatic invertebrates in wetlands. In a study of smaller wetlands spanning a range of wetland types, Holland et al. (1995) found that urbanization and drought eliminated 40 % of wetlands in a rapidly developing area of Portland, USA. Of those remaining, 25 % were severely degraded by human activities. Permanent wetlands may be less vulnerable to draining than basins with shorter hydroperiods, but they are certainly susceptible to degradation from other urban influences.

Lastly, wetlands are especially vulnerable to climate change due to their relatively shallow depths and high evaporation rates (Johnson et al. 2010). Influences of climate change on wetland ecosystems is an active area of research, with studies often using either simulations and model forecasting (Johnson et al. 2010), or comparisons among basins across a latitudinal gradient to mimic changes in climate (Kosten et al. 2012). While these are powerful approaches, we agree with Conly and Van der Kamp (2001) that careful monitoring of individual wetland ecosystems through time is also critically needed in our efforts to assess changes and preserve wetland communities in the face of climate change.

Looking Ahead

Future conservation strategies should include measures to preserve diverse, healthy faunas of aquatic invertebrates in permanent wetlands because this helps to ensure that these areas will continue to provide benefits to wetland wildlife species, but also because invertebrates are necessary in order for permanent wetlands to provide a rich suite of ecosystem services (Hanson et al. 2012). We agree with the broad view of Euliss et al. (2008) who emphasized that future wetland conservation strategies must transition from the traditional focus on wildlife values to comprehensive approaches that strive toward ensuring that permanent wetlands—and invertebrate communities—continue to provide ecosystem services that meet biological, social, political, and even economic needs. We suggest that future management frameworks must retain elements of the traditional emphasis on wildlife, yet be diversified to incorporate the roles of aquatic invertebrate communities in providing ecosystem services not historically associated with invertebrates. This broader paradigm requires a whole-wetland approach where invertebrate communities are better-integrated into studies and management at the scale of the entire wetland. Moreover, several management issues for permanent wetlands, such as increasing distributions of fish and altered hydroperiods, are influenced by factors operating outside wetland watersheds and at landscape scales. Thus, conservation of aquatic invertebrate communities in permanent wetlands will often require that management measures be directed at the wetland-watershed scale.

Our review indicates that increasing demands of agriculture and food production, urbanization, demographics, and economics are contributing to rapid declines in invertebrate communities and other ecological characteristics of permanent wetland habitats. Although permanent wetlands and shallow lakes may be drained and eliminated less frequently than smaller waters, we believe the larger, more permanently flooded wetlands remain vulnerable in temperate and tropical regions worldwide. We challenge wetland scientists and managers to explore new approaches that may help clarify roles of aquatic invertebrate communities in maintaining water quality and ecological integrity of permanent wetlands so these functions will be more widely perceived and valued by an increasingly diverse, urban society.

Appendix

Taxa of Permanent Wetlands

List of aquatic (A) macroinvertebrate and (B) microcrustacean families reported from permanent wetlands. Numbers refer to citations listed in table footnote. Full citations are given in the literature cited. Due to a lack of published information, lists of macroinvertebrates for Africa and microcrustaceans for South America were not compiled.

Taxa	Family	North America	South America	Europe	Asia	Australia
A. Macroinvertebrates						
Mollusca						
Bivalvia	Corbiculidae				22, 23	
	Mycetopodidae		21			
	Pharidae				23	
	Sphaeriidae	1, 2, 4, 8		15	23	26, 27
	Unionidae				23	26
Gastropoda	Acroloxidae			10, 12, 14		
	Ampullariidae		21			
	Ancylidae	8	21	12		25
	Bithyniidae			12, 14, 15	22, 23	
	Cochliopidae			12		
	Ellobiidae			12		
	Hydrobiidae			10, 12, 15		26, 27
	Lymnaeidae	1, 2, 4, 5, 8		10, 14	22, 23	
	Melanopsidae			12		
	Neritidae			12		
	Physidae	1, 2, 4, 5, 8	21	12, 14		26
	Planorbidae	1, 2, 4, 5, 8	21	10, 12, 14, 15	23	25, 26
	Pleuroceridae				23	
	Pomatiopsidae					25, 26, 27
	Stenothyridae				23	
	Valvatidae	2, 4		14, 15		
	Viviparidae			14	22, 23	
Annelida						
Oligochaeta	Aeolosomatidae			12		
	Enchytraeidae			15		25, 27
	Lumbricidae			12		
	Lumbriculidae	4		12		
	Naididae	4		12, 15	23	25, 26
	Phreodrilidae					25
	Tubificidae			12, 15	22, 23	25, 26, 27

(continued)

Taxa	Family	North America	South America	Europe	Asia	Australia
A. Macroinvertebrates						
Hirudinea	Erpobdellidae	2, 4		10, 15		
	Glossiphoniidae	2, 4	21	10, 15	23	25
	Haemopidae	4				
	Piscicolidae			15		
Polychaeta	Nephtyidae				23	
Chelicerata						
Acari	Arrenuridae	3				
	Eylaidae	3				26
	Hydrachnidae	3				
	Hydrodromidae	3				
	Hydryphantidae	3				
	Limnesiidae	3				25
	Limnocharidae	3				25
	Mideopsidae	3				
	Oxidae	3				25
	Pezidae					25
	Pionidae	3				
	Unionicolidae	3				
Crustacea						
Decapoda	Atyidae			12		26
	Hymenosomatidae					26, 27
	Palaemonidae		21	12	23	
	Parastacidae					25
Anaspidacea	Koonungidae					26
Amphipoda	Ceinidae					25, 26, 27
	Corophiidae			12		
	Crangonyctidae			10		
	Dogielinotidae	2, 4	21			
	Gammaridae	2, 4		10, 12, 15	22, 23	25
Isopoda	Anthuridae			12		
	Asellidae	1, 8		10, 15		
	Janiridae					27
	Scyphacidae					27
	Sphaeromatidae			12		
Tanaidacea	Leptocheliidae			12		
Hexapoda						
Collembolla	Entomobryidae	8				
	Isotomidae	1, 8				26
	Sminthuridae	8				
Insecta						

(continued)

Taxa	Family	North America	South America	Europe	Asia	Australia
A. Macroinvertebrates						
Odonata	Aeshnidae	1, 2, 3, 4, 8	19, 21	11		25
	Calopterygidae	1, 8				
	Coenagrionidae	1, 2, 3, 4, 8	19, 20, 21	10, 11, 12, 15	23	25, 26
	Dicteriadidae		21			
	Corduliidae	2, 3, 4		12		25
	Gomphidae	3	19			
	Lestidae	1, 2, 3, 4, 8	19, 21	11, 12		25
	Libellulidae	1, 2, 3, 4, 8	19, 20, 21	11, 12		25
	Perilestidae		21			
	Protoneuridae		21			
Ephemeroptera	Baetidae	1, 2, 3, 4, 8	19, 20, 21	10, 12, 15		25
	Caenidae	1, 2, 3, 4, 8	19, 20, 21	10, 12, 15		27
	Heptageniidae	3				
	Leptohyphidae		21			
	Leptophlebiidae	3	19, 21			
	Polymitarcyidae		19			
	Siphlonuridae	4				
Hemiptera	Belostomatidae	1, 3, 8	18, 20, 21			
	Corixidae	1, 2, 3, 4, 8	18, 20, 21	10, 12, 15		25, 26
	Gerridae	2, 3, 4		10, 12		
	Hebridae	3, 8	18, 21			
	Hydrometridae	3	18			25
	Mesoveliidae	2, 3, 4, 8	21	12		
	Naucoridae	3	21	12		
	Nepidae	3	18, 20			
	Notonectidae	1, 2, 3, 4, 8	18, 20, 21	10, 12		25, 26
	Pleidae	1, 3, 8	18, 20, 21	12		25
	Rhyparochromidae		18			
	Saldidae					25
	Veliidae	1, 3, 4	18	12		25

(continued)

Taxa	Family	North America	South America	Europe	Asia	Australia
A. Macroinvertebrates						
Coleoptera	Chrysomelidae	1, 2, 3, 4, 6, 8	21			
	Curculionidae	2, 3, 4, 6	21			
	Dytiscidae	1, 2, 3, 4, 6, 7, 8	18, 20, 21	10, 12		25, 26, 27
	Dryopidae		20	12		
	Elmidae	2	21			
	Gyrinidae	1, 2, 3, 4, 7, 8		15		
	Haliplidae	1, 2, 3, 4, 6, 7, 8	21	10		25
	Helophoridae	4		10		
	Heteroceridae		18			
	Hydraenidae	2, 3				
	Hydrochidae		18			26
	Hydrophilidae	1, 2, 3, 4, 6, 7, 8	18, 20, 21	10, 12		25, 26, 27
	Hygrobiidae					25
	Lampyridae		21			
	Limnichidae		18			
	Melolonthidae		21			
	Noteridae	3	18, 20, 21			
	Scirtidae	3, 4	18, 21			25
	Staphylinidae		21			26
Neuroptera	Sialidae			10		
Trichoptera	Apataniidae	2				
	Atriplectidae					26
	Brachycentridae	2				
	Calamoceratidae		19			
	Ecnomidae			12		25, 27
	Helicopsychidae					26
	Hydroptilidae	3, 4	19, 21			25
	Leptoceridae	1, 2, 3, 4, 8	19	10, 15		25, 26, 27
	Limnephilidae	2, 3, 4		10, 15		
	Molannidae	3				
	Philorheithridae					26
	Phryganeidae	1, 2, 3, 4, 8				
	Polycentropodidae	3, 4	21	15		

(continued)

Taxa	Family	North America	South America	Europe	Asia	Australia
A. Macroinvertebrates						
Lepidoptera	Crambidae	8				
	Noctuidae		21			
	Pyralidae		21			
Diptera	Ceratopogonidae	1, 2, 3, 4, 8	21	12, 15		25, 26, 27
	Chaoboridae	1, 2, 4, 8	21	15		26
	Chironomidae	1, 2, 3, 4, 8	19, 20, 21	12, 15	22, 23	25, 26, 27
	Culicidae	2, 3, 4	21	15		25
	Dixidae	2, 4	21			
	Dolichopodidae					25
	Empididae	2	21			
	Ephydridae	8	20, 21	12		25, 27
	Muscidae		20, 21			25
	Psychodidae	2, 8				25
	Ptychopteridae			15		
	Scatopsidae					25
	Sciomyzidae	4	21			
	Stratiomyidae	1, 2, 4, 8	21	12		25
	Syrphidae	2	21			26
	Tabanidae	1, 3, 4, 8	21			25
	Tipulidae	2, 4, 8	21			

Taxa	Family	North America	Africa	Europe	Asia	Australia
B. Microcrustaceans						
Diplostraca	Bosminidae	9	16	13	24	
	Chydoridae	9	16, 17	13	24	25
	Daphniidae	9	16, 17	13	24	25
	Ilyocryptidae		17			
	Lynceidae	4				
	Macrothricidae	9	16, 17			25
	Moinidae	9	17		24	
	Polyphemidae	9		13		
	Sididae	9	16, 17	13	24	

(continued)

Taxa	Family	North America	Africa	Europe	Asia	Australia
B. Microcrustaceans						
Copepoda	Ameiridae					25
	Canthocamptidae		16, 17			25
	Canuellidae		16			
	Centropagidae				24	25
	Cletodidae		17			25
	Cyclopidae	9	16, 17	13	24	25
	Diaptomidae	9	16, 17			
	Laophontidae					25
	Oithonidae				24	
	Pseudodiaptomidae				24	
	Sulcanidae					25
Ostracoda	Candonidae		16			25
	Cyprididae		16, 17			25, 26, 27
	Cytherideidae		17			
	Ilyocyprididae		17			25, 26
	Limnocytheridae					25
	Notodromadidae					25

Citations: 1 Hentges and Stewart (2010); 2 Silver et al. (2012); 3 Rosenberg and Danks (1987); 4 Hornung and Foote (2006); 5 Stephen (2006); 6 Lillie (1991); 7 Hanson and Swanson (1989); 8 Maurer (2013); 9 Norlin et al. (2006); 10 Collinson et al. (1995); 11 Carchini et al. (2007); 12 Sahuquillo et al. (2007); 13 Timms and Moss (1984); 14 Brönmark (1985); 15 Mason (1977); 16 Samraoui et al. (1998); 17 Ramdani et al. (2001); 18 Fernández and López Ruf (2006); 19 Maltchik et al. (2012); 20 Fontanarrosa et al. (2013); 21 Krawczyk et al. (2013); 22 Cai et al. (2011); 23 Cai et al. (2012); 24 Guijun et al. (2012); 25 Cale et al. (2004); 26 Khan (2003); 27 Timms (1983).

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