

Chapter 16

Invertebrates in Managed Waterfowl Marshes

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Introduction

Wetlands provide critical habitats for breeding, migrating, and wintering waterfowl. Accordingly, management agencies and conservation organizations have long-sought to improve habitats for waterfowl during key life phases through active management of wetland ecosystems. The tools used for wetland management are diverse, though most focus on the manipulation of hydrology and (or) vegetation (e.g., disking, mowing), sowing of annual plants to provide high-energy foods, or controlling vertebrate populations, such as fish or exotic mammals, that can have negative effects on management goals. Managed waterfowl marshes are unique environments, because unlike other systems explored in this volume, active wetland management for waterfowl, and hence a “waterfowl marsh” may be found in most wetland ecosystems and are ubiquitous in the northern hemisphere. Accordingly, we have adapted a broad definition of managed waterfowl marshes and review literature on a diversity of ecosystems ranging from large coastal wetlands to isolated systems, such as playa lakes or prairie potholes. In this context, we define managed wetlands as those that receive direct manipulations intended to alter the naturally occurring hydrology, vegetation, or biotic communities of the wetland (hereafter active management) with the goal of providing habitat for waterfowl during at least one phase of their annual life cycle.

There is considerable variability in the objectives, intensity, and approaches to managing wetlands as waterfowl habitat. Such management may not explicitly focus on promotion of invertebrate populations and may occur on highly variable time intervals ranging from days to decades. Combinations of many wetland management techniques are often used in an integrated strategy, and impacts of such practices are often anecdotal, particularly as they relate to aquatic invertebrate populations. For example, the widespread practice of water-level manipulation for wintering waterfowl in the southern United States is

intended to promote access to plant-based food for waterfowl, but only recently have researchers begun to understand how invertebrates respond to those manipulations and their importance for wintering waterfowl (Anderson and Smith 2000; Foth et al. 2014; Tapp and Webb 2015). Wetland management for waterfowl often conveys multiple benefits to fish, wildlife, and plant communities (Baldassarre 2014) and likely reflects practices and principles detailed in previous chapters. In this chapter, we review wetland management practices used to promote waterfowl habitat and their impacts on aquatic invertebrates in those systems.

Waterfowl Classification and Foraging Ecology

Understanding the impetus behind wetland management for waterfowl first requires a general understanding of the diversity of life-history strategies and functional morphology among waterfowl. For the purposes of this review, we focused our discussion of waterfowl to those within the family Anatidae. Anatidae is a diverse family comprising 5 subfamilies (Dendrocygninae, Anserinae, Stictonettinae, Tadorninae, Anatinae) and 171 extant species occupying all continents except Antarctica (Baldassarre and Bolen 2006). Detailed phylogenies of the group have been described elsewhere (e.g., Livezey 1997); the relevant discussion of these phylogenies for our review is to identify taxa that are likely to benefit from invertebrates in management wetlands. The first criterion for inclusion in our discussion is that the species consume invertebrates to successfully complete some part of their life-cycle. Herbivory, or more generally a plant-based diet (i.e., plant seeds and vegetation), is ubiquitous among Anatidae. The subfamily Anserinae (geese and swans) is comprised of herbivores, which exclusively forage on plant material, even during periods of high protein demand during ontogeny. Plant-dependent species also occur throughout other subfamilies within Anatidae (e.g., whistling ducks within Dendrocygninae) and many species rely on plant-dominated diets throughout most of their life cycle. The second criterion for inclusion in our discussion is that the species or taxa must consume invertebrates in habitats that are subject to management during a phase of their life cycle. Species that fall within the Mergini tribe of the Anatinae subfamily (sea ducks) for example consume considerable amounts of invertebrates in their diets but forage primarily in pelagic systems that are not subject to management. With these two criteria, our discussion focuses primarily on duck species in two subfamilies: Tadorninae (shell-ducks and torrent ducks) and Anatinae (pochards, stiff-tailed ducks, and surface-feeding ducks). Further, our discussion will be primarily constrained to species and examples within this group that occupy ranges in western Europe and North America, where most active management for invertebrates and research occurs and is relatively well documented.

Among the species meeting the above criteria, there remains considerable variability in their reliance on invertebrates. The extent of aquatic invertebrate use among waterfowl species is driven by two main factors: interspecific adaptations for foraging and interseasonal variation in nutrient demands. There are two general foraging strategies used by ducks in aquatic systems: diving and surfacing feeding or dabbling (Fig. 16.1). Diving is characteristic of sea ducks, stiff-tailed ducks, and pochards and facilitates foraging within the water column and along the benthos. Long-tailed ducks (*Clangula hyemalis*) are the deepest-documented diving ducks, having achieved diving depths in excess of 50 m (Schorger 1947), although most diving ducks likely restrict foraging to depths of 0.5 to 3 m (Baldassarre 2014). Dabbling ducks are constrained to foraging by skimming the surface, submerging their head and neck, or tipping up to submerge their head and upper body to reach foods at deeper depths - up to approximately 40 cm (Pöysä 1983). Location of foraging within the water column can have considerable influence on invertebrate use and availability among waterfowl species using varying foraging strategies. For example, midge-larvae that emerge along the water surface are consumed extensively by surface-feeding ducks, whereas benthic invertebrates such as amphipods are consumed extensively by diving ducks such as lesser scaup (*Aythya affinis*; Afton and Hier 1991).

Interspecific morphological variation among ducks has a well-documented influence on the structuring of waterfowl communities in wetlands through influences on foraging efficiency or functional foraging depths (Siegfried 1976; Pöysä 1983; Nudds and Bowlby 1984; Torrence and Butler 2006). Bill shape and structure, neck length, and body length are the primary morphological factors influencing this differentiation. The role of body and neck length and bill structure in determining foraging depths is particularly pronounced among

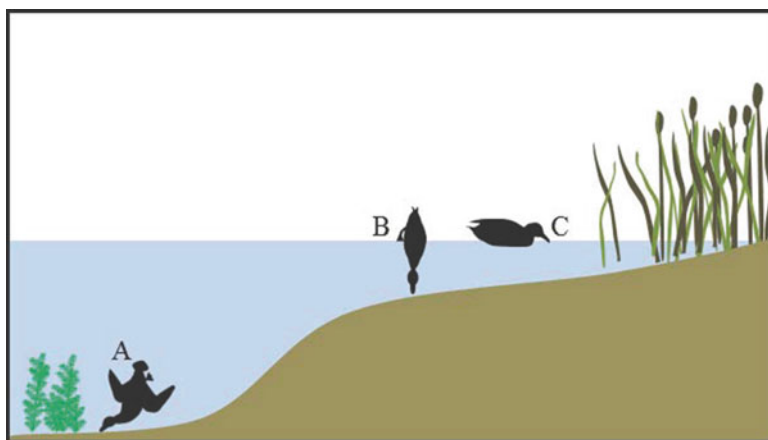


Fig. 16.1 Diving (a) and surface feeding by tipping up (b) or skimming (c) are the primary foraging habits used by waterfowl that consume invertebrates in wetlands

surface-feeding ducks, which are all characterized by elongated necks and bodies and flat bills lined with variable densities of lamellae to facilitate filtering food. Neck and body lengths influence functional feeding depths of surface-feeding ducks and facilitate depth-dependent segregation of conspecific foraging guilds in wetlands (Pöysä 1983; Pöysä et al. 1994; Isola et al. 2000). Lamellar densities among surface-feeding ducks facilitate considerable variability in invertebrate consumption; species such as mallards (*Anas platyrhynchos*) with relatively coarse lamellae densities (8 lamellae/cm) consume larger macroinvertebrates (Batzer et al. 1993), whereas northern shoveler (*Anas clypeata*) can capture and consume microinvertebrates such as rotifers because of their high-density lamellae (21 lamellae/cm) (Euliss et al. 1991). Less variability in lamellar density has been documented among diving ducks (6.7–8.3 lamellae/cm; Lagerquist and Ankney 1989) though interspecific variation in lamellar densities has been reported to contribute to structuring of conspecific foraging guilds of both surface-feeding and diving ducks in wetlands (Nudds and Bowlby 1984; Lagerquist and Ankney 1989).

Because they migrate and reproduce in highly seasonal environments, waterfowl face many energetic demands throughout their annual life cycle. Accordingly, diet can vary considerably throughout the year, depending on motivations for foraging related to major life-cycle events (e.g., ontogenesis, migration, clutch formation, feather molt) and composition and availability of prey in foraging habitats. The annual progression of the life cycle of waterfowl starting in spring is: breeding (territory establishment, clutch formation, incubation, and brood rearing); remigial feather molt in late summer; fall migration; overwintering; and finally spring migration to the breeding grounds (Fig. 16.2). Most species in our discussion are seasonally monogamous, forming pair bonds on the wintering grounds and maintaining them through spring migration and breeding. Pairs subsequently dissolve after clutches are completed and females are responsible for brood rearing independent of their mates. This life-history trait is important in considering the relative importance of invertebrates in wetlands throughout the annual cycle of males and females, which have highly variable nutrient demands within a year. In general, protein demands increase throughout spring into the breeding season; with peak invertebrate consumption on the breeding grounds and followed by a transition to plant-based (seeds and vegetative material) diets late in the breeding season and throughout the non-breeding periods (Fig. 16.2).

Migration among birds and presumably ducks is fueled almost exclusively by lipids because of its high-energy density and suitability for extramuscular storage (Jenni and Jenni-Eiermann 1998). Invertebrates are generally sought as protein sources rather than lipid or carbohydrate energy sources, which are often derived from plant-based foods. Therefore invertebrates are not consumed as much during migration as during the breeding season, except in cases of species with more carnivorous diets (e.g., lesser scaup, Anteau and Afton 2008b; Anteau et al. 2014), or those seeking to build or maintain protein reserves during migration for use in clutch formation. The tendency to transition from plant-based diets to animal-based diets late in winter and throughout spring migration in anticipation of

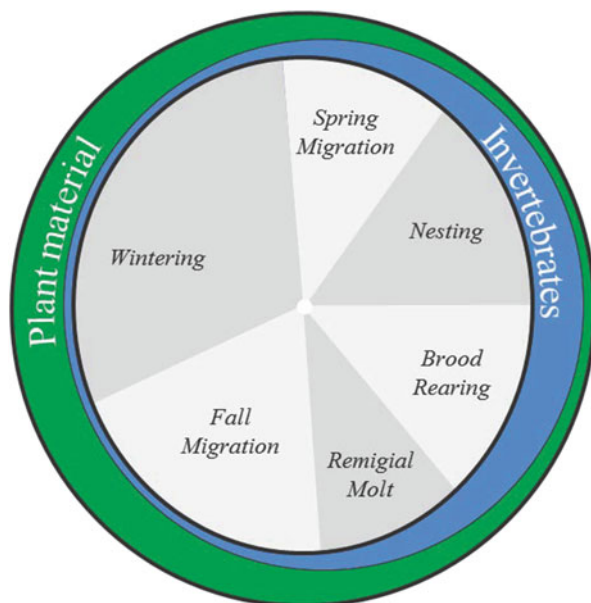


Fig. 16.2 Generalized life-cycle and diet requirements of omnivorous waterfowl. The relative size of the circle outside the life cycle illustrates the relative reliance on plant-based foods or invertebrates in waterfowl diets during each phase in their life cycle. Although many exceptions and deviations on this pattern exist, the general pattern for increasing reliance on invertebrates during the breeding season and plants-based foods during the non-breeding season holds across many omnivorous waterfowl species

nutrient demands for reproduction has been documented in many species (e.g., Euliss and Harris 1987), with some dabbling ducks selectively foraging on invertebrates disproportionate to their availability in wetlands during spring migration (Tidwell et al. 2013).

Waterfowl lay relatively large, nutrient-rich eggs and therefore incur substantial protein and lipid costs during clutch formation, which are often satisfied by invertebrate consumption on the breeding grounds or reserve accumulation prior to arrival on the breeding grounds (Ankney et al. 1991; Alisauskas and Ankney 1992). Duck diet studies ranging from generally herbivorous species, such as gadwalls (*Anas strepera*; Ankney and Alisauskas 1991) or canvasbacks (*Aythya valisineria*; Bartonek and Hickey 1969), to carnivorous species, such as lesser scaup (Afton and Hier 1991) or northern shovelers (Ankney and Afton 1988), have consistently illustrated the ubiquity of invertebrate consumption during the breeding season. Protein, and therefore invertebrate demands, remain throughout the breeding season associated with ontogenic growth of precocial young, which depart the nest and begin feeding on invertebrates (aquatic and emerging adults) within 24 h of hatching (Sedinger 1992). Distribution and abundance of aquatic invertebrates during brood rearing periods can influence habitat use, behavior and growth rates of broods and individual ducklings and, thus, are often the focus

of wetland management strategies in breeding habitats (Hunter et al. 1984; Cox et al. 1998).

Protein demands also increase after breeding when adult (>second year) males and females undergo synchronous replacement of flight feathers during the remigial molt. This synchronous molting strategy of waterfowl renders them flightless for periods of 2–7 weeks (Hohman et al. 1992) during which selection for wetlands with abundant invertebrate food sources has been documented for some species (Kohler and Kohler 1998). After completion of the remigial molt, waterfowl initiate fall migration and most species rely on plant-based diets that are often subsidized by grains in agricultural fields. Use of invertebrates during this period appears to be restricted to species with carnivorous diets (e.g., lesser scaup; Afton et al. 1991) or those constrained to large water bodies (Ross et al. 2005). Plant-based diets tend to persist throughout the wintering period in many species until the aforementioned shift from plant-based diets to invertebrates occurs in anticipation of spring migration or breeding. Despite the prevalence of plant material in waterfowl diets during fall and winter, invertebrate consumption during the period is ubiquitous (e.g., Baldassarre et al. 1983; Euliss and Harris 1987; Ballard et al. 2004) and is likely necessary to derive essential amino acids for metabolism or for maintenance and synthesis of somatic tissues (Loesch and Kaminski 1989; Heitmeyer and Fredrickson 1990; Richardson and Kaminski 1992).

Goals of Waterfowl Management in Wetlands

The three principle motivations for wetland management for waterfowl are (1) provision of space for non-foraging activities (i.e., courtship and pair formation, or roosting) (2) facilitating waterfowl-based recreation (i.e., observing or hunting) and (3) provision of food for foraging waterfowl. These three motivations are rarely mutually exclusive and the focus of this chapter is on the final motivation (food) so we only briefly mention the first two (space for waterfowl and (or) recreation) to provide context for some wetland-management programs targeting waterfowl that may not emphasize food resources as a desired management outcome. Management focused on provision of space for waterfowl seeks to provide either roosting habitats, refuges from hunting pressure during fall and winter, or nesting cover. As alluded to earlier, many waterfowl shift from wetland food resources to terrestrial food resources, generally in the form of waste agricultural seeds, throughout the non-breeding period. However, these species still seek out and use wetlands for roosting and supplemental foraging habitats, which can become limiting in some landscapes (Fox et al. 1994; Anteau et al. 2011b). Accordingly, some wetland management strategies aim to provide suitable roosting cover for waterfowl without any explicit concern for food within those habitats. Another common objective for wetland management during the non-breeding season is to provide refuge from anthropogenic disturbances (primarily hunting)

for migrating or wintering waterfowl (Madsen 1995; Knapton et al. 2000). In general, most ducks included in our discussion nest in upland habitats around wetlands and use wetlands only for foraging or roosting. However, some species nest over water in wetland vegetation and therefore have specific nesting habitat requirements that can be the focus of wetland management practices (e.g., red-heads, *Aythya americana*; Low 1945).

Many waterfowl-based wetland management strategies aim to increase abundance of food resources for waterfowl during at least one period of their annual life cycle. Wetland management for invertebrates and waterfowl is the focus of this chapter, so we will only briefly mention the context of that management, and provide more detail on methods and results later. In general, wetland management practices for waterfowl foods overwhelmingly focus on the manipulation of vegetation or hydrologic regimes to promote early successional plant communities capable of producing large quantities of carbohydrate-rich seeds for waterfowl during the non-breeding period. Primary waterfowl breeding habitats in northern temperate and arctic latitudes, where invertebrates are most important in the diet, are rarely subject to management control, whereas wetland complexes used during non-breeding periods at mid- and southern latitudes, where waterfowl consume mostly plant-based diets, are often subject to substantial annual management control. Despite the overall focus on plant-based foods in many waterfowl management practices, invertebrate community responses to plant-focused manipulations are increasingly recognized at southern latitudes (e.g., Gray et al. 1999; Davis and Bidwell 2008; Foth et al. 2014; Tapp and Webb 2015) and some management and conservation efforts are ongoing at northern latitudes with the intention to increase invertebrate abundance in wetlands used by migrating or breeding waterfowl (e.g., Hornung and Foote 2006; Anteau and Afton 2008a; Anteau et al. 2011a).

An additional motivation for wetland management relevant to waterfowl aims to attract waterfowl or influence their distribution to satisfy wetland and waterfowl-based recreationists, such as observers, photographers, or hunters. Such management engages a broad constituency, can foster strong sociopolitical and financial support for wetland conservation (e.g., Enck et al. 1993; Adams et al. 1997; Vrtiska et al. 2013), and may provide positive local economic impacts that strengthen support for wetland conservation (Gren et al. 1994; Grado et al. 2001). Nongovernmental organizations with recreation-based constituencies, such as Ducks Unlimited, Inc. in North America, have made substantial contributions to wetland conservation and in raising public awareness and support for wetland conservation issues beyond those relevant exclusively to recreational endeavors (Tori et al. 2002). Widespread public interest in waterfowl conservation, driven strongly by waterfowl hunters in the case of North America (Organ et al. 2010), along with the international migratory behavior of waterfowl across the world has led to the development of many international conservation strategies with net benefits for wetlands and aquatic invertebrates therein. For example, since its inception in 1986, the North American Waterfowl Management Plan (NAWMP) and

associated funding support mechanisms in the United States, Canada, and Mexico have expended over \$4 billion (USD) on conservation of over 63,000 km² of wetland habitats throughout North America (NAWMP 2012). A comparable international agreement and conservation strategy exists in Eurasia (African-Eurasian Waterbird Agreement) to identify conservation priorities for Eurasian waterfowl and other wetland-dependent birds.

Where Wetlands Important to Waterfowl Occur

Wetlands of importance to waterfowl occur in many regions of the Northern Hemisphere, and in North America in particular. Their geographic location may partly relate to their importance in providing invertebrate forage. In the United States, wetlands most subject to active waterfowl management tend to occur in the mid- and southern latitudes. Key regions include California's Central Valley, wetlands of the Great Basin region in Oregon, Nevada, and Utah, the Playa Lakes region of Texas, the Mississippi Alluvial Valley, the Upper Mississippi River and its associated pools and wetlands, and Nebraska's Rainwater Basin. Within most of these areas large wetland complexes (e.g., Bear River Migratory Bird Refuge in Utah) are managed primarily for waterfowl and other migratory birds and, therefore, are well suited to the provision of plant and animal foods. Other regions, such as the Mississippi Alluvial Valley, comprise predominantly small, privately owned wetlands (e.g., rice fields) that provide habitat for migrating and wintering waterfowl. Breeding habitats at more northern latitudes in the United States and Canada, including the Prairie Pothole Region, the Boreal Forest, and Arctic region of Canada and Alaska, are keystone habitats for waterfowl, but because of their geographic isolation and extreme climatic variability, receive little direct active management for waterfowl.

Hagy et al. (2014) reviewed wetland conservation issues of relevance to waterfowl in Latin America. They concluded that most priorities involved inventorying existing wetland areas and bird populations; management of wetlands at meaningful scales in this region (for invertebrates or otherwise) was not a common priority. Numerous important wetland systems exist for waterfowl outside of North America, but many are not subject to management consideration. Much of coastal United Kingdom and continental Europe and Africa contain thousands of areas deemed critical wetland habitats for migratory waterfowl, most of which are accounted for and may be investigated using the Critical Site Network Tool and associated publications (<http://wow.wetlands.org/INFORMATIONFLYWAY/CRITICALSITENETWORKTOOL/tabid/1349/language/en-US/Default.aspx>). Notable regions include the Camargue Region of France, the Ebro Delta of Spain, and the rice-growing regions of Australia and Japan. Wetland areas in Argentina are often subject to waterfowl hunting, but

the extent of wetland management on these sites is poorly documented (Ferreyra et al. 2014). Many of these regions are associated with rice or other agriculture subject to flooding, although managed marshes exist in some regions, especially the Camargue, that provide important foraging habitats for migratory waterfowl (Arzel et al. 2009).

Unfortunately, little has been written on management of wetlands outside of North America for invertebrate production for waterfowl. Most studies of invertebrates and waterfowl in these other regions describe associations between duck use and invertebrate abundances (e.g., Phillips 1991), foraging ecology (e.g., Giles 1990), or diet (e.g., Mouronval et al. 2007). Similarly, critical networks of wetlands for waterfowl exist throughout Asia, Australia and New Zealand, Africa, and the Indian Subcontinent, but the extent of management for invertebrates in these regions is largely undocumented. Detailing the international scope of wetlands managed for waterfowl would be untenable for this chapter; therefore, we focus on general ecological principles of wetland management that should broadly apply to invertebrate communities and waterfowl, acknowledging that the majority of examples and insights are of North American studies.

Wetland Management Strategies

Wetland management for waterfowl takes many forms that can generally be classified into three strategies; hydrologic manipulations, direct-vegetation manipulations, and biotic manipulations (of vertebrates). Use of these strategies is rarely exclusive and they are often implemented simultaneously in systems ranging from geographically isolated wetlands such as Playa Lakes or prairie wetlands to coastal or riverine wetlands. Similarly, a wide gradient of management intensity exists with two extremes spanning from systems that may receive management on decades-long return intervals to those that receive active manipulations or management on intraannual (seasonal) or perhaps even daily time-scales. For example, as we discuss in detail below, efforts to eradicate fish populations in prairie wetlands over a few years can have long-lasting positive impacts that favor improved waterfowl habitat for many years after active management has occurred. In contrast many wetland management strategies for waterfowl use seasonal or even monthly/weekly management of vegetation or water levels based on fine-tuned understanding of seasonal habitat needs of waterfowl. Our discussion focuses primarily on active management strategies applied on annual time scales, but we also discuss longer-term management strategies, specifically related to biotic manipulation of vertebrates or invasive species in managed wetlands.

Hydrologic Manipulations

Hydrologic manipulations in wetlands are typically achieved using levees containing water control structures with the capacity to introduce or remove water from the wetland (Fredrickson and Taylor 1982; Gray et al. 1999). Examples of water control structures include screw and flap gates and flash-board (also referred to as drop-board) risers (Gray et al. 2013). Water can be introduced to manage wetlands through gravity-flow water source from a higher elevation or through use of gas or electric pumps capable of moving water across elevation gradients and into managed wetlands (Gray et al. 2013).

Water-level manipulations in wetlands are often done for a variety of management objectives related to providing favorable water depths for foraging water birds, eliciting a vegetative response, or promoting dry soil conditions that allow for additional management activities such as direct-vegetation or soil manipulations (Fredrickson and Taylor 1982; Isola et al. 2000; Taft et al. 2002; Greer et al. 2007). Within seasonal wetlands managed for early successional moist-soil plant communities, water levels are typically reduced during spring, to provide suitable conditions for germination and growth of annual grasses, sedges, rushes, and forbs. These plants are fast growing, reach sexual maturity quickly (i.e., <3 months), and produce large quantities of seeds with relatively high nutritional quality for dabbling ducks (Haukos and Smith 1993; Gray et al. 1999). To reduce monocultures of perennially emergent plants, including cattail (*Typha* spp.) and phragmites (*Phragmites australis*), which are also poor producers of seeds for waterfowl, managers of prairie wetlands often periodically draw down water levels in late spring every 4–6 years (Merendino et al. 1990; Gray et al. 2013). This water-level manipulation disrupts the life-history needs of these two wetland species, allowing other plants to recolonize.

Within managed wetlands, the duration and timing of inundation, or hydroperiod, as well as depth of flooding, can influence macroinvertebrate abundance, species richness, community composition, and production (Batzer and Resh 1992). However the relationship between hydroperiod and invertebrate community response is not consistent among wetlands types and has resulted in contradictory results (Neckles et al. 1990; Schneider and Frost 1996; Hall et al. 2004; Batzer 2013). For example, temporary and seasonal wetlands in California with longer hydroperiods had greater invertebrate diversity and abundance for some taxa (Batzer and Resh 1992), whereas hydroperiod explained minimal variation in invertebrate metrics within seasonal woodland wetlands in northern Minnesota and Wisconsin (Palik et al. 2001; Batzer et al. 2004; Hanson et al. 2010). Alternatively, emergent invertebrate taxonomic richness, biomass, and production peaked in riparian wetlands along the Platte River with intermediate hydroperiods, compared to sites with longer or shorter hydroperiods (Whiles and Goldowitz 2001). The contradictory results of numerous studies examining the relationship between wetland hydrology and invertebrate communities led Batzer (2013) to conclude that while hydrology, and specifically hydroperiod,

was clearly important in structuring invertebrate communities within seasonally flooded wetlands, generalization about the direction and strength of this relationship was likely confounded by the sensitivity of invertebrates to other environmental factors (e.g., water and air temperature, water depth and chemistry, predators, etc.).

Hydroperiod can indirectly influence wetland invertebrate diversity and production by supporting populations of vertebrate predators, which are often implicated as a primary factor structuring wetland invertebrate communities (Schneider and Frost 1996; Corti et al. 1997; Wissinger 1999). Depending on the water source, inundating wetlands and maintaining water levels for longer time periods allows for the colonization and survival of fish, which prey on invertebrates (Batzer and Resh 1992). Wetlands with shorter hydroperiods or those that are drawn down more frequently typically support lower vertebrate predator densities, especially fish (Batzer and Wissinger 1996). In a study that simultaneously evaluated effects of hydroperiod and predation on Mississippi River floodplain invertebrate communities, total invertebrate taxa richness, abundance, and biomass were lower in sites with more predators and the strength of this relationship increased with duration of floodplain inundation (Corti et al. 1997). Schneider and Frost (1996) reported greater abundance and diversity of predators in vernal ponds with longer hydroperiods and subsequent increased effects of biotic interactions, particularly predation, on invertebrate populations.

The timing of spring water-level drawdowns in managed wetlands influences the macrophyte community composition, with earlier drawdowns often resulting in germination of moist-soil plant species capable of producing large biomasses of seeds (Fredrickson and Taylor 1982; Gray et al. 2013). However, there is also potential for early drawdowns to preclude invertebrate taxa with longer life-history stages (Wilbur 1987; Neckles et al. 1990). Wetlands with shorter hydroperiods, or those drawn down earlier in the spring, may restrict presence of some species because they are unable to complete the aquatic portion of their life cycle before water is removed from the wetland or they lack capacity to survive longer dry periods in desiccation-resistant life stages (Schneider and Frost 1996; Corti et al. 1997). In addition, managed wetlands with differing hydrology or spring drawdown dates exhibit distinct temporal patterns of insect emergence, which can result in varying peaks of adult insect biomass availability along a temporal gradient (Whiles and Goldowitz 2001).

Late-summer inundation of managed seasonal wetlands can influence invertebrate communities: Anderson and Smith (2000) reported the greatest invertebrate abundance and biomass in playas flooded in September (compared to later November inundation) and Batzer et al. (1993) found greater densities of benthic midge larvae in moist-soil wetlands inundated earlier in autumn. Although both studies noted that earlier flooding schedules did not necessarily reflect natural conditions, early fall flooding is sometimes implemented by wetland managers to create inundated wetland habitat for autumn migrating shorebirds and early migrating dabbling ducks (Batzer et al. 1993; Anderson and Smith 2000).

Wetland hydrology is often manipulated to directly alter macrophyte distribution, structure, and community composition, which in turn can influence aquatic invertebrate communities, making it challenging to separate the effects of manipulating hydroperiod and vegetation on invertebrates (Fredrickson and Taylor 1982; Batzer and Resh 1992; Hall et al. 2004; Batzer 2013). Hydrologic variation is the driving force structuring diversity and production of wetland plants, which increase structural habitat for invertebrates, serve as refugia from predators, provide attachment sites, and produce detritus consumed by many invertebrates (Batzer and Wissinger 1996). Whiles and Goldowitz (2001) reported greatest plant species richness and production at Platte River wetlands with intermediate levels of flood duration and speculated that the high invertebrate species richness and production at these same sites could be linked to macrophyte communities. In an experimental study that manipulated wetland plant density, de Szalay and Resh (2000) found greater macroinvertebrate diversity in areas with high densities of emergent plants, but also reported greater overall invertebrate abundance and lower diversity in open water areas. Given that invertebrate communities vary with wetland plant species composition, as well as varying structure or density within the same plant species, it is challenging to understand and differentiate the effects of various wetland management practices on aquatic macroinvertebrates (Olson et al. 1995; Streever et al. 1995; Batzer 2013).

Direct-Vegetation Manipulations

Wetland vegetation may be manipulated to achieve habitat objectives for migrating waterbirds, and these techniques strive to set back plant succession to enhance overall seed production and improve water-cover ratios. Such techniques also may influence abundance and diversity of aquatic invertebrates. Common manipulations include prescribed burning (Fig. 16.3a), grazing, mowing, and disking of soils, sometimes in conjunction with planting agricultural grains. Davis and Bidwell (2008) reported that wetlands experiencing these different types of vegetation manipulation yielded similar aquatic invertebrate richness and diversity, although these metrics were generally greatest in grazed wetlands and least in disked wetlands. Notably, plant biomass in mowed areas was less than unmanipulated areas, supporting the need to leave some vegetation intact (Davis and Bidwell 2008). Although direct manipulations didn't offer a distinct advantage in enhancing invertebrate communities, the authors suggested direct manipulations were reasonable given management objectives of controlling nuisance plant species and enhancing seed production (Davis and Bidwell 2008). In a study evaluating autumn invertebrate communities in managed, seasonally inundated wetlands in the Lower Mississippi Alluvial Valley, Tapp and Webb (2015) reported no effects of mowing on invertebrate biomass or family richness but did find invertebrate production was approximately ten times greater on sites that were mowed.



Fig. 16.3 These photos illustrate two types of active wetland management for waterfowl habitat conducted by the US Fish and Wildlife service at the 130 km² Horicon National Wildlife Refuge in southeastern Wisconsin, USA. Figure (a) depicts the use of prescribed fire as a direct-vegetation manipulation intended to increase availability of open foraging habitats and macrophyte diversity in a 1200 ha wetland impoundment that was completely dominated by cattail vegetation. Figure (b) shows a trap full of carp in the Rock River that feeds the wetland complex. The trap uses an electronic barrier and vertical bars in the river to capture and remove carp moving upstream to spawn (Photos courtesy of USFWS)

Gray et al. (1999) reported that aquatic invertebrate biomass and diversity was greatest in mowed and control plots in moist-soil units in Mississippi, with tilled and disked plots generally being least in these metrics. In a study of an experimentally manipulated cattail marsh, Murkin et al. (1982) reported invertebrate populations were unaffected by various treatments to manipulate vegetation cover-water ratios, but noted that dabbling duck pair densities were correlated positively with invertebrate biomass on treated plots. Overall, direct manipulations of vegetation appears to have mostly neutral influences on invertebrate biomass and diversity, with potentially positive effects on production, and thus appear to be a reasonable practice when such manipulations obtain other desirable management objectives.

Bio-manipulation

Wetland management strategies designed to manipulate vertebrate populations to improve wetland functioning or suitability for waterfowl are often termed bio-manipulation. The most common of these practices focus on the management of fishes because the presence of fishes can have a strong influence on invertebrate composition and nutrient dynamics in wetland food webs. Aquatic invertebrates are generally less abundant in wetlands that harbor fish populations owing to direct predation by fish, changes in phytoplankton and macrophyte communities, or a combination of both (Mallory et al. 1994; Hanson and Riggs 1995; Parkos et al. 2003). In wetlands of the Prairie Pothole Region (PPR), the presence of fish had a greater influence on macroinvertebrate composition than surrounding land-use attributes (Tangen et al. 2003). It has even been suggested that the absence of fishes can promote greater richness of aquatic birds, plants, amphibians and invertebrates in small, isolated wetlands (Scheffer and van Geest 2006). Thus, the introduction and (or) management of fishes in wetlands raises important concerns among wildlife biologists because of potential interactions between fishes and waterfowl.

Wetland macroinvertebrates represent important food resources for both fish and waterfowl. In a South Dakota study, diets of spring-migrating lesser scaup were similar (92%) to those of yellow perch (*Perca flavescens*), an intensively managed sport fish (Strand et al. 2008). Fishes can also have important indirect effects on wetland invertebrate communities. The presence of fish in a New York marsh resulted in reduced abundance of snails and midge predators, but greater abundance of epiphytic midges owing to indirect effects of fish on competitive/predatory release from other invertebrates (Batzer et al. 2000). Although a variety of fishes are known to inhabit wetlands and shallow lakes, two species in particular—fathead minnow (*Pimphales promelas*) and common carp (*Cyprinus carpio*)—have been well studied with regard to their effects on food web structure and nutrient cycling in shallow lakes and wetlands and provide a good case-study of the role of biotic manipulations in wetland management for waterfowl.

Fathead Minnow

The fathead minnow is widely distributed in central North America (Scott and Crossman 1973) and has been introduced to many areas along the Atlantic and Pacific coast drainages in the United States (Andreassen 1975). Commonly found in wetlands, fathead minnow densities can reach over 350,000/ha (Duffy 1998). Because fathead minnows are a valued baitfish, they are easily moved among waterbodies via “bait bucket” introductions by anglers. Fathead minnow are also commonly harvested from wetlands and sold to commercial bait dealers (Duffy 1998). In palustrine wetlands of eastern South Dakota, the annual wholesale value of fathead minnows averaged about \$232/ha in the early 1990s (Carlson and Berry 1990).

The effects of fathead minnow on wetland invertebrates have been well documented (see Zimmer et al. Chap. 8 of this volume). Early work in Minnesota showed that invertebrate abundance, biomass, and taxon richness were lower in wetlands containing fathead minnows (Hanson and Riggs 1995). Similarly, a study of 19 semi-permanent wetlands in west-central Minnesota showed that invertebrate community structure was affected by fathead minnow abundance, wetland depth, and abundance of aquatic macrophytes, with fathead minnow being the most influential parameter measured (Zimmer et al. 2000). In addition to reducing invertebrate abundance, fathead minnows are known to affect other important biotic and abiotic attributes in wetlands (Anteau and Afton 2008a; Anteau et al. 2011a). In the eastern PPR, wetlands that contained fathead minnows had fewer cladocerans, calanoid copepods, ostracods, and larval tiger salamanders but greater turbidity, total phosphorus, and chlorophyll-*a* concentrations (Zimmer et al. 2001, 2002). Because fathead minnows often represent a dominant species in wetlands where fish occur, they can have strong ecosystem effects that influence plant and invertebrate abundance (Zimmer et al. 2002)—that ultimately affects waterfowl use. Mallard ducklings, for example, grew and survived better in fishless wetlands compared to wetlands that contained fathead minnow (Cox et al. 1998).

Common Carp

Native to Europe and Asia, the common carp has been introduced worldwide and is found on every continent except Antarctica (Weber and Brown 2009). In North America, common carp are often a dominant species in shallow lakes and riverine wetlands and are considered by biologists as a nuisance species with regard to waterfowl management in wetlands. A survey of National Wildlife Refuge managers in the United States revealed that 80% of refuges with wetland impoundments identified common carp as a management challenge (Ivey et al. 1998). The benthivorous feeding behavior of adult carp can have direct, “bottom-up” effects on aquatic systems that results in increased nutrient concentration, greater turbidity, and reduced submerged macrophyte abundance (Parkos et al. 2003). Similarly, nutrient enhancement via excretion and (or) increased decomposition of aquatic macrophytes can increase turbidity and have profound effects on ecosystem state

(i.e., clear- or turbid-water state; Scheffer et al. 1993). In Great Lakes wetlands, carp-related turbidity above 20 nephelometric turbidity units was associated with fewer submerged plant species (mean=2.6 plants) than observed in wetlands with lower turbidity (mean=10.5 plants; Lougheed et al. 1998).

Life-history attributes of common carp, such as rapid growth and early maturation, contribute to their success in introduced environments, where they can rapidly expand to reach high biomass (>3000 kg/ha; Weber and Brown 2009). In experimental wetlands, total phosphorus, turbidity, and suspended solids were positively related to carp biomass (175–476 kg/ha), whereas macrophyte and macroinvertebrate abundance decreased with increasing carp biomass (Parkos et al. 2003). Early life stages of common carp (<100 mm total length) are known to consume zooplankton (Meijer et al. 1990), but effects of common carp on zooplankton densities are often equivocal. Common carp have been associated with increases (Drenner et al. 1998; Parkos et al. 2003) and decreases (Lougheed et al. 1998) in zooplankton biomass. At sizes greater than 100 mm, common carp switch to foraging on benthic macroinvertebrates and detritus and can reduce benthic invertebrate abundance and diversity. In a recent review, Weber and Brown (2009) found that in 94% of the surveyed literature, benthic macroinvertebrates decreased in response to common carp. Invertebrate taxa that are negatively influenced by common carp include amphipods, annelids, chironomids, and odonates (Miller and Crowl 2006; Weber and Brown 2009; Anteau et al. 2011a). Both predation (Kloskowski 2011) and reduction of macrophytes (Matsuzaki et al. 2007) are believed to be responsible for the reduction of invertebrate biomass in carp-invaded communities.

The establishment of common carp has long been implicated in the disappearance of aquatic macrophytes and reduction of waterfowl use in shallow lakes and wetlands (Bajer et al. 2009). At biomass concentrations of <30 kg/ha, carp were shown to have no effect on macrophytes or waterfowl abundance in Illinois wetlands. However, when carp biomass exceeded 250 kg/ha, vegetative cover declined by 17% and waterfowl use was only 10% of that documented before carp became established (Bajer et al. 2009). Similarly, Ivey et al. (1998) estimated that carp invasion in Malheur National Wildlife Refuge in Oregon reduced waterfowl production there to 25% of the level observed prior to carp invasion. Because fishes such as carp and fathead minnow can have dramatic effects on wetland plants, invertebrates, and waterfowl, a variety of management approaches have been developed to aid in control or removal of these wetland fishes (Fig. 16.3b).

Control/Manipulation of Wetland Fish Populations

Biomanipulation is a common technique used to improve water quality and ecosystem functioning in eutrophic lakes and wetlands. In a review of biomanipulation techniques commonly applied to fish assemblages, Drenner and Hambright (1999) found that partial fish removal was the most successful technique (90%) in improving water quality and habitat conditions for plants and aquatic invertebrates. In a related study of 18 Dutch shallow lakes, removing less than 70% of fish biomass

had no impact on water turbidity, but in lakes where fish biomass was reduced below 30% of their initial abundance, water clarity improved appreciably (Drenner and Hambright 1999). Other techniques, such as piscivorous fish stocking (26% of studies reviewed), piscivore stocking with partial fish removal (60%), and elimination of fish followed by re-stocking (67%) generally appear to be less successful at combating eutrophication (Drenner and Hambright 1999).

In efforts to restore waterfowl populations in Lake Christina, Minnesota, the lake was chemically treated with rotenone in the late 1980s to reduce the abundance of benthivorous fish (primarily carp). Early responses to fish removal showed that the cladoceran community shifted from small-bodied taxa (e.g., *Bosmina* spp.) to larger cladoceran taxa (e.g., *Daphnia* spp.) within 6 months (Hanson and Butler 1990). Concomitant with changes in zooplankton composition, chlorophyll-*a* concentrations declined and water transparency and submergent macrophytes increased dramatically (Hanson and Butler 1990). Three years post-treatment, use of Lake Christina by migrating waterfowl increased significantly, presumably due to changes in macroinvertebrate abundance and submerged plants (Hanson and Butler 1994). Although reductions in fish biomass can have profound effects on plant-invertebrate-waterfowl interactions in wetlands, they are generally not permanent because over time, because fish populations increase via recruitment, invasion, and (or) introductions. For example, Lake Christina has been chemically treated three times in the last 40 years to reduce effects of benthivorous fish. Similar efforts to reduce carp populations through direct removal or through rotenone treatments in systems managed for waterfowl are ubiquitous across the United States and report variable long-term success (Fig. 16.4; e.g., Cahoon (1953) at Lake Mattamuskeet in North Carolina or Weier and Starr (1950) in coastal marshes in Ohio).

Stocking of piscivorous fish, such as walleye (*Sander vitreus*), has been used to control fathead minnow populations in wetlands. Fisheries managers in the PPR often use semi-permanent and permanent wetlands to temporarily rear juvenile walleye, thus providing an opportunity to evaluate effects of walleye stocking on wetland attributes. In Minnesota wetlands, the stocking of walleye fry (12,000 fry/ha) resulted in significant reductions in fathead minnow populations (Herwig et al. 2004; Ward et al. 2008). In addition, walleye stocking resulted in increases in water clarity, cladoceran abundance, and some macroinvertebrates whereas phytoplankton biomass declined (Reed 2006; Potthoff et al. 2008; Fig. 16.4). Changes in biotic and abiotic wetland attributes following stocking of walleye fry was attributed to their rapid diet shift from invertebrates to small fish (i.e., fathead minnows). As with fish removal techniques, however, effects of walleye stocking can be short-lived, requiring repeated re-stocking to maintain desired wetland conditions (Potthoff et al. 2008).

Other Biomanipulations

Fish are the most commonly manipulated vertebrates in wetlands managed for waterfowl because of their direct and indirect impacts on food web structure. However, other vertebrates are often targeted for reduction (or removal) in efforts

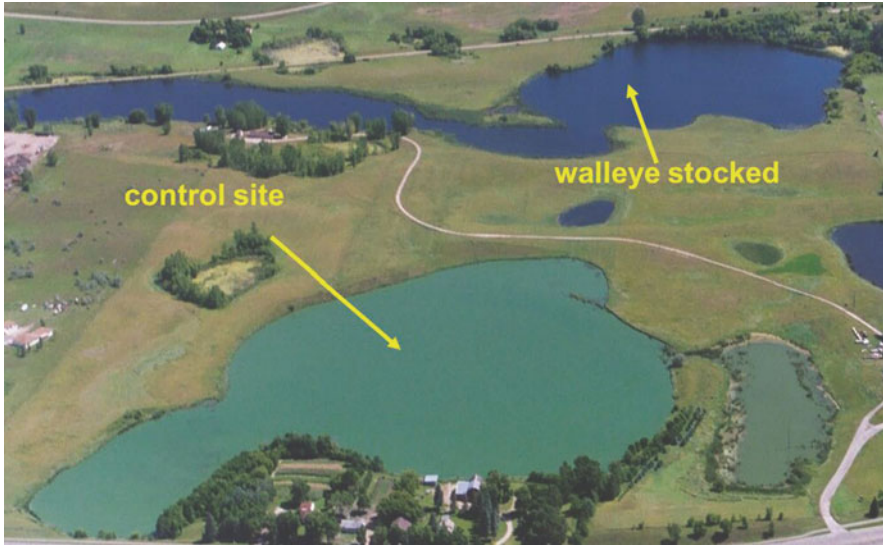


Fig. 16.4 Stocking walleye fingerlings to reduce fathead minnow abundance has proven to be an effective management strategy for improving wetland habitat and water quality in Prairie Pothole wetlands. By reducing fathead minnow abundance, walleyes impose a trophic cascade, resulting in increased water clarity, submerged macrophytes, and greater macroinvertebrate abundance. Below are two wetlands—one stocked with walleye to reduce fathead minnow density (walleye stocked) and one that contains only fathead minnows (control site). Photo courtesy of B. Herwig, Minnesota Department of Natural Resources

to improve wetland conditions for waterfowl. Aquatic mammals have received considerable attention in this respect where a variety of strategies have been used to manage their populations in waterfowl marshes. Muskrats (*Ondatra zibethicus*) and beavers (*Castor canadensis*) for example can be “friend or foe” to wetland managers and are often a focus of habitat management strategies. Beavers and muskrats have well-documented roles in improving waterfowl habitat in wetlands through their impacts on water levels (Beard 1953; see beaver wetlands Chap. 12 of this volume) and vegetation density and composition (Clark 2000; de Szalay and Cassidy 2001), respectively. Further, habitat heterogeneity created by beavers may influence aquatic invertebrates, such as increasing diversity (Hood and Larson 2014). However, conflicts between these species and wetland management objectives often exist and can become the focus of population reduction efforts. The most common conflicts between wetland managers and beavers relate to construction of dams in areas that interfere with water control structures—beavers often respond to drawdowns in managed systems by constructing dams on outlet pipes. Similarly, muskrat populations can be of management concern in cases where their abundance has negative impacts on desired vegetation within a wetland or because of their tendency to construct burrows in the steep slopes of dikes around wetland impoundments. Considerable design and engineering efforts go into abating the latter of these issues related to the optimal slope and dimensions of dikes around impoundments or through burying fence to prevent burrowing into dikes.

Nutria (*Myocastor coypus*) is another aquatic mammal garnering increased attention among wetland managers in North America. Nutria were imported to several states for fur production during the 1930s, and were also deemed useful as a means to control undesirable aquatic vegetation (Carter and Leonard 2002). Since this time, nutria have become well established in the wild in several North American states, and are most abundant along the Gulf Coast and in Oregon (Carter and Leonard 2002). Nutria can cause crop damage, destroy wetland infrastructure via burrowing (e.g., undermining levees), and have been implicated in the loss of coastal wetlands in Louisiana through direct vegetation damage. Therefore, nutria likely indirectly influence wetland invertebrate populations through the removal of important vegetation and substrates, and destruction of wetland infrastructure. Fortunately, control techniques, such as trapping and toxicants, exist to reduce nutria populations where they have become problematic.

Ironically, another emerging threat for waterfowl habitat in North America comes from an exotic species of waterfowl, the mute swan (*Cygnus olor*) which was introduced from its native range in Europe (Petrie and Francis 2003). Mute swans are increasingly a concern for wetland and waterfowl managers across a diversity of ecosystems because of their impacts on aquatic plant productivity and potential indirect effects on invertebrate populations. Many studies have shown reductions in aquatic macrophytes in wetlands associated with grazing by mute swans (e.g., Allin and Husband 2003; Tatu et al. 2007; Stafford et al. 2012); however, the direct effects of such grazing on macroinvertebrates in these wetlands are equivocal (e.g., Allin and Husband 2003) and understudied. Direct control efforts on mute swans have been conducted in some systems though such efforts are often met with controversy from the general public (Ellis and Elphick 2007).

Controversies and Challenges

Of controversies facing wetland management for waterfowl, we suggest the foremost is the notion that active waterfowl management, for invertebrates and otherwise, promotes static, artificial situations intended to maintain consistent hydrology and cover-water ratios that approximate 50:50 (i.e., hemi-marsh; Weller and Spatcher 1965). Various studies support the notion that waterfowl abundance in breeding, migratory, and wintering regions is greatest in wetlands where cover-water interspersions approach even ratios (Kaminski and Prince 1984; Smith et al. 2004; Webb et al. 2010). However, these intended recommendations may work against normal wetland hydrologic cycles, resulting in wetlands that are less productive or functional over the long-term, which may impede ecosystem health and services. Recent clarifications to wetland management concepts have encouraged more natural manipulations (e.g., use of fire) and hydrology under controlled situations. Nonetheless, the mandate to manage migratory birds may create a mismatch in wetland quality and productivity, and we suggest this topic requires specific study on the costs and benefits of such practices. We note, however, that wetland

complexes, properly managed, may rotate through various stages; thus, in some situations static conditions may be more easily avoided.

Another important and contemporary challenge to waterfowl management for invertebrates is accessibility of water for active wetland management. This is of recent and particular importance in the western United States, where many states can experience drought conditions that lead to conflicts for water use. Regions that actively manage wetlands (e.g., in the Klamath Basin; Burke et al. 2004) face pressure on providing water for wetland management given urban and agriculture requirements in the area and downstream. In arid areas, wetlands that remain unflooded during breeding or migration may result in considerable losses of waterfowl habitat, and prolonged dry periods exacerbate the need for solutions to water shortages that address ecological and anthropogenic demands (Burke et al. 2004). Water banks, where water is temporarily purchased from willing sellers for specific uses, may provide one mitigation option, but long-term solutions are evasive (Burke et al. 2004).

Perhaps the greatest challenge to effective wetland management to provide invertebrates for waterfowl is the lack of consistent and conclusive trends identified by previous research on the environmental factors and ecological processes that influence wetland invertebrate communities (Batzer 2013). Inability to detect consistent patterns in invertebrate response to wetland management practices may be because invertebrates, which are tremendously diverse taxa, are simultaneously influenced by numerous ecological and environmental factors including detritus, hydrology, water chemistry, and predation (Batzer 2013). Many studies have evaluated effects of wetland management on invertebrate biomass and community composition, however invertebrate secondary production, or the formation of animal biomass over time, is less commonly evaluated and the dynamics of aquatic invertebrate populations are likely an important element to consider when determining the implications of wetland management for waterfowl (Anderson and Smith 2000; Whiles and Goldowitz 2001; Tapp and Webb 2015). Secondary production of invertebrate communities incorporates invertebrate abundance, biomass, growth, and even colonization of different invertebrate taxa, which may make it a useful metric to evaluate overall invertebrate response to wetland habitat management strategies (Benke and Huryn 2010). Studies of aquatic invertebrates are challenging, time-consuming, and often costly; however, this frontier in wildlife and wetland research needs to be explored more fully if best management practices are to be science-driven. Research on waterfowl selection of different invertebrate groups relative to different life-history events may provide more insight into when and where invertebrates as a food resource are most limiting, and which should be the focus of management. In addition, variation inherent in invertebrate communities make active management for invertebrates difficult, and recommendations, management strategies, and best practices are lacking. The dearth of information may be apparent from our literature review, and we believe new emphasis be focused on bottom-up processes that relate to invertebrate communities with respect to active and passive wetland management practices (Box 16.1).

Box 16.1: Neonicotinoids: An Emerging Threat to Invertebrate Communities in Managed Wetlands?

Neonicotinoids are a class of pesticide developed in the 1980s that have been widely adopted for agricultural use throughout North America and Europe, in large part because they are selectively more toxic to insects than vertebrates (Kollmeyer et al. 1999; Tomizawa and Casida 2005), and their use has grown considerably since 2000 promoted by their flexible use, and systemic (uptake by the plant) activity (Goulson 2013). However, >90 % of active ingredients found in neonicotinoids applied as seed treatments enter the soil, where half-life can range from 200 to >1000 days (Goulson 2013). Given the relatively long half-life and high degree of water solubility of many neonicotinoids, repeated application has the potential to accumulate high concentrations in soils, which can then leach to groundwater or surface water following precipitation events (Gupta et al. 2008; Starnner and Goh 2012). Recently, neonicotinoids were detected in >90 % of wetlands sampled within the prairie pothole region of Saskatchewan (Main et al. 2014), whereas Hladik et al. (2014) reported neonicotinoid occurrence in all Midwestern streams sampled, many with concentrations exceeding acute and chronic exposure levels for aquatic macroinvertebrates. In addition to receiving neonicotinoids indirectly through hydrologic inputs from the surrounding watershed, managed wetlands also have the potential for increased neonicotinoid concentrations through direct application as part of moist-soil management practices. Portions of managed wetlands are sometimes planted with agricultural grains (usually corn) as part of the soil disturbance to reset vegetative successional patterns (though disking action) and provide an alternative, high carbohydrate food source for dabbling ducks, however if managers use neonicotinoid-treated seed, direct application of these insecticides has the potential to influence wetland macroinvertebrate communities.

Beketov et al. (2008) demonstrated that a single-pulse application of the neonicotinoid thiacloprid altered long-term community structure of stream macroinvertebrates in a mesocosm, with populations of longer-lived species less likely to recover. A study in the Netherlands reported a significant negative correlation between imidacloprid concentrations in surface waters and macroinvertebrate abundance, including orders Diptera and Ephemeroptera, which commonly occur in wetland ecosystems (Van Dijk et al. 2013). However, this study relied on disparate, previously collected data, where invertebrate and neonicotinoid samples were collected in different locations (up to 1 km apart) and times (up to 160 days apart) (Van Dijk et al. 2013). Prolonged exposure in water to the neonicotinoid imidacloprid was linked to changes in growth, persistence, and community composition of aquatic invertebrates, particularly to individuals in the functional group known as shredders, potentially reducing ecosystem functions related to decomposition, nutrient cycling, and water quality (Kreutzweiser et al. 2009; Agatz et al. 2014; Chagnon et al. 2015). Currently, little is known on neonicotinoid concentrations in managed wetlands and the potential to impact on aquatic invertebrate communities, however if results of lab studies translate to field conditions, direct application of neonicotinoid-treated seeds in managed wetlands could pose an emerging threat to wetland invertebrates.

Conclusions

Invertebrates in managed wetlands ([Appendix](#)) clearly provide valuable food resources for waterfowl during all portions of the annual cycle. Because many species rely on proteinaceous foods prior to and during nesting, and young feed almost exclusively on aquatic invertebrates, management to promote these resources may be particularly valuable. However, it appears that invertebrate production for waterfowl is often a consequence of other wetland management practices intended to promote desirable vegetation and carbohydrate-rich foods. Correspondingly, few studies have involved invertebrate production in managed waterfowl marshes, although this topic is beginning to receive more attention.

Managed wetlands for waterfowl occur globally, but we have focused on those in North America and Europe. However, wetland management strategies vary considerably even within close geographic areas. Hydrologic manipulations are common, which involve controlling hydroperiods and extent of inundation to achieve desired results. These techniques may influence macroinvertebrates, but results are inconsistent. Direct manipulations of vegetation may also affect invertebrate abundances and diversity, but likely provide results similar to unmanaged wetlands. Vertebrates may also be managed to “biomanipulate” wetlands. Fish, in particular fathead minnows and common carp, can negatively influence invertebrate abundance, biomass, and richness in wetlands of importance to waterfowl. These species may be subject to control, thereby improving water quality, ecosystem function, and invertebrate populations. Finally, other vertebrate species, such as mute swans and nutria, may alter wetland habitats in a fashion that negatively impacts invertebrate foods for waterfowl. It may also be desirable to control these species.

Wetland management for waterfowl may create long-term artificially static hydrologic patterns with the potential to negatively impact wetland ecosystem processes. Efforts are ongoing to improve hydrologic practices for waterfowl. Issues of availability of water resources for wetland management affect many regions, especially in western North America. Climate change could exacerbate these issues and present important socioeconomic and ecological challenges. Finally, the influence of waterfowl habitat management on invertebrates remains poorly understood, and a unified approach, perhaps in the context of adaptive resource management, would improve understanding and efficiency of management strategies for waterfowl.

Appendix

Aquatic invertebrates collected from waterfowl marshes across North America.

	Manitoba, Canada	California, USA	California, USA	Prairie Pothole Region, USA and Canada	US Central Prairie	Mississippi Alluvial Valley, USA	Mississippi Alluvial Valley, USA	Rainwater Basin, Nebraska, USA
NEMATODA	X		Sacramento National Wildlife Refuge ^c	Throughout ^d	X	Greentree reservoirs and flooded forests ^f	Seasonally inundated wetlands with herbaceous vegetation ^g	Playa wetlands ^{h,i}
CNIDARIA					X			
TURBELLARIA					X			
ROTIFERA				X	X			
MOLLUSCA					X			
Gastropoda								
Hydrobiidae			X	X				
Lymnaeidae	X			X	X			X
Physidae	X		X	X	X	X	X	X
Planorbidae	X			X	X	X	X	X
Valvatidae				X				
Bivalvia								
Sphaeriidae					X	X		X
ANNELIDA								
Oligochaeta	X							
Lumbriculidae				X	X		X	X
Naididae				X			X	X
Tubificidae				X				
Hirudinea				X				
Erpobdellidae				X	X			X

(continued)

(continued)

	Manitoba, Canada	California, USA	California, USA	Prairie Pothole Region, USA and Canada	US Central Prairie	Mississippi Alluvial Valley, USA	Mississippi Alluvial Valley, USA	Rainwater Basin, Nebraska, USA
	Lake Manitoba Experimental Cells ^a	Suisun Marsh ^b	Sacramento National Wildlife Refuge ^c	Throughout ^d	Platte River ^e	Greentree reservoirs and flooded forests ^f	Seasonally inundated wetlands with herbaceous vegetation ^g	Playa wetlands ^{h,i}
Glossiphoniidae	X			X	X			X
CRUSTACEA								
Branchiopoda								
Artemiidae				X				X
Bosminidae				X				
Branchinectidae							X	
Chirocephalidae				X				
Chydoridae					X			
Daphniidae			X	X	X			X
Lynceidae				X				
Thamnocephalidae								X
Branchiura								
Copepoda	X	X		X			X	X
Calanoida			X					
Cyclopoida			X					
Ostracoda	X	X	X	X				X
Amphipoda	X							X
Crangonyctidae					X			
Dogielinotidae	X			X	X			X
Gammaridae	X			X			X	X

(continued)

	Manitoba, Canada	California, USA	California, USA	Prairie Pothole Region, USA and Canada	US Central Prairie	Mississippi Alluvial Valley, USA	Mississippi Alluvial Valley, USA	Rainwater Basin, Nebraska, USA
	Lake Manitoba Experimental Cells ^a	Suisun Marsh ^b	Sacramento National Wildlife Refuge ^c	Throughout ^d	Platte River ^e	Greentree reservoirs and flooded forests ^f	Seasonally inundated wetlands with herbaceous vegetation ^g	Playa wetlands ^{h,i}
Ceratopogonidae	X		X	X	X		X	X
Chaoboridae			X	X				X
Chironomidae	X	X		X		X	X	X
(Chironominae)		X	X	X	X			
(Tanypodinae)			X	X	X			
(Orthocladinae)		X	X	X	X			
Culicidae	X	X	X	X	X	X	X	X
Dolichopodidae			X					
Dixidae			X	X			X	X
Empididae			X					
Ephydriidae	X	X	X		X		X	
Muscidae			X		X			
Psychodidae								X
Sciaridae					X			
Sciomyzidae			X		X			
Simuliidae			X					
Stratiomyidae			X	X	X	X	X	X
Syrphidae						X		

Tabanidae											X
Tipulidae/ Limoniidae	X										X
Hymenoptera											
Pteromalidae					X						

^aMurkin and Ross (2000)
^bde Szalay and Resh (1997)
^cHicks et al. (1997)
^dEuliss et al. (1999)
^eWhiles (unpublished)
^fFoth (2011)
^gTapp and Webb (2015)
^hRiens et al. (2013)
ⁱT. Schepker and E. Webb (unpublished data)

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