Chapter 1
An Introduction to Freshwater Wetlands and Their Invertebrates

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This text assembles prominent wetland ecologists from across the globe to describe the ecology of the invertebrates residing in the wetlands they each study. Each of their chapters assumes the reader has some basic knowledge about wetland ecology and about invertebrates. Because some may not have this background, we have prepared a brief introductory chapter to familiarize people with some basic aspects of freshwater wetland habitats and provide some foundational information about the invertebrate fauna that exploits freshwater wetlands.

Defining Wetlands

Despite the fact that wetland ecology is now a well-established scientific discipline, what defines a "wetland" habitat remains inconsistent worldwide. Perhaps the most widely used international definition comes from the *Ramsar Convention on Wetlands*, which reads:

> Wetlands are areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine water the depth of which at low tide does not exceed six metres. (www.ramsar.org)

This definition is very broad and includes many habitats, such as shallow lakes and reservoirs, that might not be considered wetlands in many localities. It is primarily meant for a nonscientist audience and lacks the functional mechanistic aspect attractive to ecologists.

In the USA, the history of wetland definition has had a convoluted past (see Sharitz et al. 2014), largely because regulations there confer special protections to and restrictions on wetlands. Thus, what is or is not called a wetland can be controversial. A fairly narrow definition has been adopted, coined by the *US Army Corps of Engineers*, the primary agency charged with regulating US wetlands, which reads:

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> The term “wetlands” means those areas that are inundated or saturated by surface or ground water at a frequency and duration sufficient to support, and that under normal circumstances do support, a prevalence of vegetation typically adapted for life in saturated soil conditions. Wetlands generally include swamps, marshes, bogs, and similar areas. (http://el.erdc.usace.army.mil/elpubs/pdf/wlman87.pdf)

This definition has been interpreted to mean that appropriate hydrology, vegetation, and hydric soils *all* need to be present at a site for it to be legally called a wetland and eligible for certain governmental protections. Like the Ramsar definition, it is not an ecological definition, but instead one intended to be used for legal purposes and of course only in the USA. However, it does address how hydrology, vegetation, and soils interact to produce wetland conditions. But for many, the US definition is unnecessarily narrow as it excludes habitats that would be considered wetlands by most ecologists such as non-vegetated mudflats or floodplain areas that routinely flood but still lack hydric soils (e.g., Fig. 1.1).

In Europe, wetland definition is complicated by the diversity of national traditions surrounding the habitats. The most widely accepted definition was developed for the Water Framework Directive (WFD CIS 2003), which reads:

> Wetlands are heterogeneous but distinctive ecosystems which develop naturally or are the product of human activities. Their biogeochemical functions depend notably on a constant or periodic shallow inundation by fresh, brackish or saline water, or saturation at or near the surface of the substrate. They are characterised by standing or slowly moving waters. Common features include hydric soils, micro-organisms, hydrophilous and hygrophilous vegetation and fauna, adapted to chemical and biological processes reflective of periodic or permanent flooding and/or water-logging.

This definition is clearly ecological in nature and expands beyond hydrology, vegetation, and soils to also address microbes and animals. The term *pond* is also widely used in Europe, which is defined as “a waterbody with a maximum depth of no more than 8 m, offering water plants the potential to colonise almost the entire area of the pond” (Oertli et al. 2005). Wetland invertebrate ecologists in Europe have embraced this convention because their organisms of interest are focal components of pond ecosystems. Shallow ponds would be considered wetlands worldwide, but at least in the USA, areas of ponds that are >2 m depth and lack macrophytes would be labeled as deepwater habitats rather than wetlands (Cowardin et al. 1979).

For this book, our goal is to develop an international flavor to the study of wetland invertebrates, and we recognize that what habitats are considered wetlands varies worldwide (even beyond the examples we cite). Thus, we do not impose a specific definition of what constitutes a wetland, nor what constitutes a wetland invertebrate, instead relying on the discretion of the chapter authors. However, most ecologists recognize that wetlands are largely defined by climate, hydrology, and vegetation and that the resident invertebrate faunas are controlled by these factors.

Fig. 1.1 Floodplain of the Oconee River, Georgia. While this habitat floods most years, most of its expanse is not considered *jurisdictional wetland* using criteria of the US Army Corps of Engineers (Environmental Laboratory 1987) because most soils are not hydric and flooding occurs primarily in winter outside the "growing season" for plants. Reprinted with permission from *Ecology of Freshwater and Estuarine Wetlands: Second Edition*, edited by Darold P. Batzer and Rebecca R. Sharitz. © 2014 by the Regents of the University of California. Published by the University of California Press

Defining Wetland Invertebrates

Aquatic invertebrates from a number of animal phyla thrive in wetlands including Turbellaria (flatworms), Rotifera (rotifers), Nematoda (roundworms), Annelida (segmented worms and leeches), Mollusca (snails and clams), and Arthropoda (crustaceans, mites, insects). Ecologists studying aquatic invertebrates in wetlands tend to focus either on microinvertebrates (microturbellarians, rotifers, nematodes, small crustaceans) or macroinvertebrates (large flatworms, annelids, mollusks, large crustaceans, mites, insects). These two size-based groupings have no scientific standing and to some extent simply reflect how the organisms are sampled and habitats they use. By convention a microinvertebrate is <1 mm long, and a macroinvertebrate is >1 mm long, and this metric was largely established by the mesh size of the nets most often used to sample the organisms (coarse mesh for macros and fine mesh (<1 mm) for micros). But obviously, this size-based metric is problematic; for example, an early stage macroinvertebrate (e.g., second instar midge larva) might be <1 mm, but would still be labeled a macro. Possibly more important than actual body size is habitat utilization. Planktonic organisms are mostly microinvertebrates suspended in the water column, where they are sampled using plankton tows or fine-mesh sweep nets. Most macroinvertebrates, in contrast, are associated with various substrates, including the bottom sediments and plant surfaces (benthos) or the water's surface (neuston), where they are usually sampled with corers and coarse-mesh sweep nets. However, numerous exceptions to this dichotomy exist. Microinvertebrates such as nematodes and rotifers are mostly benthic, as are many species of microcrustaceans. On the other hand, several macroinvertebrate species inhabit the water column such as the freshwater jellyfish (*Craspedacusta sowerbii*), fairy shrimps (Anostraca), and phantom midges (Chaoboridae). Considering macroinvertebrates and microinvertebrates separately is purely arbitrary, and efforts addressing both micro- and macroinvertebrates would obviously be optimal. However, such holistic approaches remain rare largely due to more extensive sampling and processing costs (almost double) and also to a lack of taxonomic expertise by most researchers to deal with the full range of organisms.

The Aquatic Macroinvertebrate Fauna

Batzer and Ruhí (2013) recently assembled data on macroinvertebrates from 447 freshwater wetlands from across the globe to assess which taxa tended to dominate these habitats, at least in terms of occurrence. Table 1.1 lists the 40 macroinvertebrate families that occurred in at least 10 % of those 447 wetlands (another 135 less common taxa were also recorded). The list of common taxa includes 25 insects, 5 annelids, 4 crustaceans, 4 molluscans, 1 acarine (water mites), and 1 turbellarian, indicating that insects are by far the most diverse group in wetlands. Among the 25 insect families, 8 families were Diptera (flies), 5 were Hemiptera (water bugs), 4 were Coleoptera (water beetles), 4 were Odonata (damselflies and dragonflies), 2 were Ephemeroptera (mayflies), and 2 were Trichoptera (caddisflies). This is in stark contrast to the aquatic insect faunas in streams, where assemblages are dominated by Ephemeroptera, Plecoptera (stoneflies), and Trichoptera.

Batzer and Ruhí (2013) found that the Chironomidae (midges) and Dytiscidae (predaceous diving beetles) were the only families that were virtually ubiquitous across the 447 wetlands (Table 1.1). Corixidae (water boatmen), Hydrophilidae (water scavenger beetles), and Oligochaeta (aquatic worms) also occurred in most (>50 %) of the wetlands. Remarkably, most macroinvertebrate taxa occurred only in a relatively small subset of available wetlands, although where they occurred, these less-widespread taxa can still be very abundant and ecologically important.

Table 1.1 Forty aquatic macroinvertebrate taxa that had ≥10 % occurrence across a set of 447 wetlands worldwide (from a meta-analysis by Batzer and Ruhí 2013)

Family[a]	Order/class	Percent occurrence	Dry phase strategy	Respiration	Feeding functions: primary/ secondary
Chironomidae	Diptera	97.3	D, M	C	C/P
Dytiscidae	Coleoptera	87.5	D, M	SA	P
Corixidae	Hemiptera	69.1	M	SA	P/C
Hydrophilidae	Coleoptera	67.1	M	SA/C	P
Oligochaeta[a]	Oligochaeta	58.6	D	C	C
Acarina[a]	Acarina	49.2	D, M	C	P/C
Ceratopogonidae	Diptera	46.5	D	C	P/C
Culicidae	Diptera	46.5	D, M	SA	C
Notonectidae	Hemiptera	45.9	M	SA	P
Libellulidae	Odonata	45.2	D, M	G	P
Limnephilidae	Trichoptera	41.6	D	G/C	Sh/P
Haliplidae	Coleoptera	39.6	D, M	SA/C	Sh
Sphaeriidae	Bivalvia	38.9	D	G	P
Physidae	Gastropoda	38.3	D	SA	Sc
Coenagrionidae	Odonata	38.0	M	G/C	P
Planorbidae	Gastropoda	37.6	D	SA	Sc
Baetidae	Ephemeroptera	36.0	M	G	C
Chaoboridae	Diptera	33.8	D, M	C	P
Lestidae	Odonata	29.5	D	G	P
Lymnaeidae	Gastropoda	28.6	D	SA	Sc
Lumbriculidae[b]	Oligochaeta	28.2	D	C	C
Turbellaria[a]	Turbellaria	27.5	D	C	P
Gerridae	Hemiptera	26.8	M	SA	P
Tipulidae/Limoniidae	Diptera	26.8	M	SA	Sh/C
Glossiphoniidae	Hirudinea	22.1	D	C	P
Gyrinidae	Coleoptera	20.4	M	SA/G	P
Aeshnidae	Odonata	19.2	M	G	P
Dixidae	Diptera	18.1	D, M	SA	C
Tubificidae[b]	Oligochaeta	17.9	D	C	C
Asellidae	Malacostraca	17.4	D	C	C/Sh
Tabanidae	Diptera	17.0	D, M	SA	P
Stratiomyidae	Diptera	16.1	D, M	SA	C
Erpobdellidae	Hirudinea	14.8	D	C	P
Dogielinotidae	Malacostraca	13.8	D	G	C/Sh
Caenidae	Ephemeroptera	11.9	M	G	C
Lynceidae	Diplostraca	11.4	D	C	C
Leptoceridae	Trichoptera	10.7	M	C	P/C
Pleidae	Hemiptera	10.5	M	SA	P

(continued)

Table 1.1 (continued)

Family[a]	Order/class	Percent occurrence	Dry phase strategy	Respiration	Feeding functions: primary/ secondary
Crangonyctidae	Malacostraca	10.3	D	G	C/P
Belostomatidae	Hemiptera	10.3	M	SA	P

The last three columns indicate (1) each group's strategy for dealing with drought (*D* desiccation tolerance, *M* migration), (2) each group's primary mode(s) of respiration (*SA* surface air breathers, *C* cutaneous, *G* gills), and (2) each group's primary and secondary feeding functions (*C* collecting, *P* predation, *Sc* scraping, *Sh* shredding)

[a] Oligochaeta, Acarina, and Turbellaria are not families, and these categories include all families for those groups. These higher taxa were used because many authors do not report the families involved

[b] Lumbriculidae and Tubificidae are families in Oligochaeta, so these data also contributed to the table under that classification

The Aquatic Microinvertebrate Fauna

The microinvertebrates of wetlands are studied less than the macroinvertebrates, particularly the meiobenthos. Compositions of microinvertebrates in planktonic and benthic habitats differ markedly. In the water column, planktonic rotifers and microcrustaceans dominate in terms of biomass and species richness. Along wetland substrates, nematodes are the dominant microinvertebrates, although microturbellarian flatworms, Gastrotricha (hairy backs), Tardigrada (water bears), as well as some rotifers and microcrustaceans can be abundant (Rundle et al. 2002) and productive (Anderson et al. 1998). Species richness of nematodes is particularly high, with 605, 327, and 160 species being described in freshwater of Europe, Africa, and North America, respectively (Traunspurger 2002), with many more species as yet undescribed. While often considered planktonic, most rotifers and cladocerans (water fleas) are actually benthic (Margalef 1983; Wetzel 2001).

Ecological roles of planktonic and benthic microinvertebrate communities also differ. Feeding by planktonic microcrustaceans and rotifers can control phytoplankton primary production (Scheffer et al. 1993). In turn, planktivorous and piscivorous fishes can affect zooplankton productivity either directly or indirectly via trophic cascades (sensu Hairston et al. 1960). In this sense, planktonic microinvertebrates become focal to pelagic food webs (Angeler et al. 2003). Feeding by meiobenthos on microbes in biofilms can affect bacterial composition, biomass, or production, again via direct or indirect pathways (Hakenkamp et al. 2002). These impacts on wetland bacteria can affect biochemical processes such as cellulose degradation (Toyohara et al. 2012).

The Terrestrial Invertebrate Fauna

While the aquatic invertebrate fauna has garnered the most research attention, wetland habitats also can support a rich terrestrial invertebrate fauna (myriapods, spiders, mites, beetles). The terrestrial faunas in floodplains (see Chaps. 13 and 14) and peatlands (see Chap. 7) seem especially well developed. The terrestrial fauna is dominated by plant and soil associates. While caterpillars and other herbivorous insects feed on the leaves of wetland macrophytes and trees, the fact that these plants happen to occur in wetlands is not particularly relevant to the ecology of these invertebrates; thus, we do not expand on these invertebrates here. However, the terrestrial invertebrates living in and on the soils of wetlands are subject to periodic flooding and thus must be specifically adapted to tolerate inundation to thrive in wetlands. Just as a habitat-specific aquatic invertebrate fauna exists in wetlands, a habitat-specific terrestrial invertebrate fauna also appears to exist in wetlands (Bright et al. 2010). Many nonaquatic invertebrates in wetlands can survive being underwater for extended periods (Rothenbücher and Schaefer 2006), and some millipedes and spiders have the ability to respire aquatically (Adis 1986; Pedersen and Colmer 2012).

Complete descriptions of terrestrial invertebrate assemblages in wetlands are lacking, and existing research tends to focus on a few groups. Braccia and Batzer (2001) described invertebrate assemblages associated with submersed wood in a floodplain and found terrestrial mites (especially Oribatida), springtails (Collembola), and various wood-associated beetle larvae and adults to be widespread. Mites associated with wood and leaf litter are very widespread in forested floodplains of the Southeastern USA and can readily tolerate flooding. Numerous species of ants (Formicidae) occur in wetlands, and the economically important imported fire ant (*Solenopsis invicta*) of South and now North America is a wetland-associated taxon (Ahrens et al. 2005). In peatlands, ant mounds are focal points for the emissions of greenhouse gases (carbon dioxide and methane) (see Chap. 7; Wu et al. 2013). A diversity of ground beetles (Carabidae) occurs in wetlands, and in Europe carabids are being used as bioindicators of the ecological health of floodplains (Greenwood et al. 1991; Boscaini et al. 2000) and peatlands (Holmes et al. 1993). Spiders are important predators in a host of wetlands (e.g., Jordan et al. 1994; Denno et al. 2002).

Wetland Hydrology and Invertebrates

Because hydrology, controlled by climate, ultimately structures wetland environments, specific wetland types can often be categorized by their water budgets (Jackson et al. 2014). For any particular wetland, knowing which water inputs and water outputs control the hydrology of the habitat can provide useful ecological insights. How water enters and leaves a wetland is summarized in Fig. 1.2 and the following water budget equation:

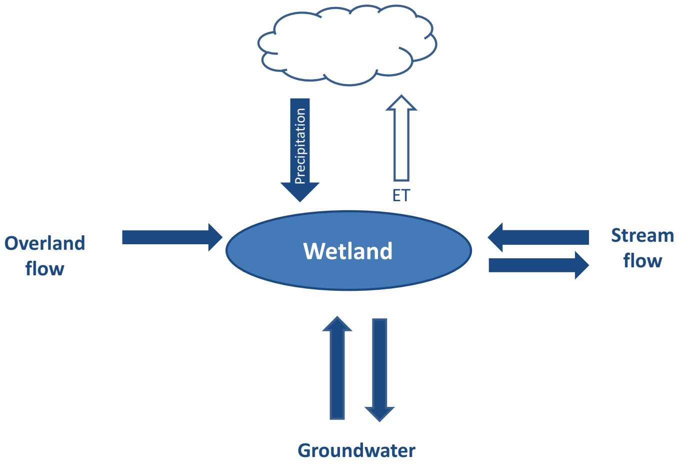

Fig. 1.2 Cartoon depicting the major water inputs and outputs to wetlands

$$P + GW_{in} + \mathrm{OF}_{\mathrm{in}} + \mathrm{SF}_{\mathrm{in}} = \mathrm{ET} + \mathrm{GW}_{\mathrm{out}} + \mathrm{OF}_{\mathrm{out}} + \mathrm{SF}_{\mathrm{out}} + \Delta V$$

where

P = volume of precipitation falling on the wetland
ET = evapotranspiration from the wetland
$\mathrm{GW}_{\mathrm{in}}$ = volume of groundwater flow into the wetland
$\mathrm{GW}_{\mathrm{out}}$ = volume of groundwater flow leaving the wetland
$\mathrm{OF}_{\mathrm{in}}$ = volume of overland flow into the wetland
$\mathrm{SF}_{\mathrm{in}}$ = volume of stream/river flow into the wetland
$\mathrm{SF}_{\mathrm{out}}$ = volume of stream/river flow leaving the wetland
ΔV = change in water volume (or storage) per unit time.

Wetlands in general can be classified into precipitation-, overland flow-, groundwater-, or stream flow-based habitats. Examples of wetlands highlighted in this book that are primarily filled by precipitation include temperate seasonal ponds (Chap. 4), Mediterranean climate ponds (Chap. 5), some peatlands (e.g., bogs, Chap. 7), and rock pools (Chap. 2). Evapotranspiration tends to be the largest avenue of water output from precipitation-based wetlands. Examples of overland flow-based wetlands include alpine wetlands (Chap. 3) and northern seasonal ponds filled by snowmelt. Examples of groundwater-based wetlands include most permanent and semipermanent marshes (Chap. 8), lakeshore marshes (Chap. 9), some peatlands (fens, Chap. 7), turloughs (Chap. 6), and of course groundwater springs and seeps (Chap. 11). Permanently flooded wetlands are typically tied to surficial groundwater aquifers. Examples of wetlands filled by stream or river flow include temperate and tropical floodplains (Chaps. 13 and 14) and beaver wetlands (Chap. 12). Some wetlands defy simple hydrologic categorization such as the Florida Everglades (Chap. 10) where water inputs from direct precipitation, river flow, and groundwater are all important. Managed wetlands such as constructed wetlands (Chap. 15) and managed waterfowl marshes (Chap. 16) often rely on engineered water sources that can include precipitation, groundwater, overland flow, and/or stream/river flow. Even wetland types dominated by one major source of water usually also receive water from secondary sources. Because most aquatic invertebrates congregate in the lowest-lying areas of wetlands where water persists, the longest, secondary sources of water (e.g., groundwater) can often be very important to controlling the ecology of the invertebrate fauna.

Besides water budgets, a wetland's *hydroperiod* (or hydropattern or hydroregime) is an important way to hydrologically categorize habitat (Jackson et al. 2014). Hydroperiod refers to the amount of time surficial, standing water is present in a wetland, regardless of the source. Because invertebrates primarily live in association with the surficial water of wetlands, hydroperiod is an especially important factor controlling them. Wissinger (1999) maintained that five different aspects of hydroperiod combine to control aquatic invertebrate populations and communities, including:

1. Water permanence (permanent vs. semipermanent vs. temporary)
2. Predictability of filling (unpredictably, seasonally, over climatic cycles)
3. Seasonality of filling and drying
4. Duration of wet and dry phases
5. Harshness of wet or dry phases (extremes in temperature and desiccation)

Figure 1.3 summarizes how these various aspects of hydroperiod manifest in different wetland types.

Understanding how each of Wissinger's five aspects of hydroperiod can affect invertebrates yields valuable information about community controls.

1. *Water permanence* is a primary control on invertebrates because if a wetland dries, the permanent water species are eliminated (although they can recolonize) while those with desiccation resistance strategies can persist. Invertebrates in permanent waters can be large, slow-developing taxa, while those in temporary waters must be smaller, fast-developing taxa (Wellborn et al. 1996). Further, water permanence and the presence of invertivorous fish are often correlated.
2. *Predictability* is important to invertebrates because if filling or drying is very unpredictable and brief (e.g., ephemeral wetlands), only highly opportunistic species that can rapidly exploit newly created habitat and develop quickly in brief periods of inundation will occur (e.g., floodwater mosquitoes). But if patterns of drying and filling are very predictable (e.g., in vernal pools), a plethora of invertebrate taxa may adapt their life cycles to match that hydroperiod (e.g., anostracan fairy shrimp, dragonflies and damselflies, limnephilid caddisflies).
3. *Seasonality* is important to invertebrates because as ectotherms they are strongly regulated by temperature. If a wetland fills in summer when temperatures are high, then active flying insects (e.g., odonates, hemipterans) can readily colonize, and all invertebrate types can complete development rapidly. In contrast, if a wetland fills in winter when temperatures are low, few aerial colonists would

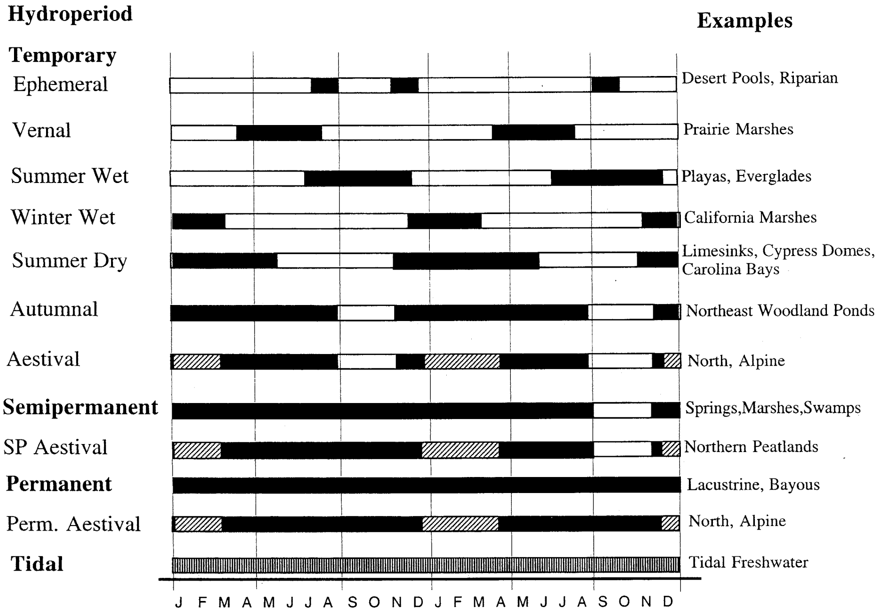

Fig. 1.3 Schematic showing different patterns of flooding and drying in representative wetlands of North America (listed on *right side* of the diagram). Dark bars indicate periods of flooding, and white bars periods of drying over a hypothetical 2 year period. *Hatched bars* indicate when the water column in boreal wetlands might freeze to the bottom in winter. Reprinted with permission from *Ecology of Freshwater and Estuarine Wetlands: Second Edition*, edited by Darold P. Batzer and Rebecca R. Sharitz. © 2014 by the Regents of the University of California. Published by the University of California Press

be active, and development of any invertebrates would be slow, requiring a long duration of flooding for them to succeed.

4. *Duration* of the wet period is important to invertebrates because some species can develop rapidly and exploit even very short duration hydroperiods (e.g., microcrustaceans, fly larvae), while others require many months to develop (e.g., large dragonfly nymphs and beetle larvae) and are only successful in long duration hydroperiods. Similarly, duration of the dry phase is also important because if the dry period is very long (months or years), only a few invertebrate species may be able to persist, but if short (days or weeks), even species poorly adapted to withstand desiccation might still cope.
5. *Harshness* of the wet or dry phase may impose additional constraints on invertebrates. In warm tropical or subtropical wetlands such as the Everglades (see Rader 1999), high water temperatures may stress invertebrates, either directly or via reduced oxygen supplies. In cold climates, invertebrates in seasonally dry wetlands in winter must withstand both desiccation and freezing, and even if a wetland is not dry in winter, the entire water column may still freeze (see Wissinger et al. 1999). In arid or semiarid climates, the substrates of wet-

lands may completely desiccate during dry phases permitting the diapause stages of only a few taxa to persist (Anderson et al. 1999). In contrast, in humid environments, substrates may remain moist even after surface water disappears, and a range of strategies by invertebrates to withstand drying may still be effective (see Ruhí et al. 2013).

The classic paper by Wiggins et al. (1980) categorizes how different aquatic invertebrates exploit annual temporary pools using as criteria the various strategies they employ to deal with wetland drying, including the ways they tolerate or avoid drought, how they disperse (passively vs. active aerially), and the seasonality of dispersal and oviposition. They devised four types:

1. *Overwintering residents.* These organisms can tolerate drought but lack active dispersal and thus occur in the wetlands year-round (in some form). Prominent examples include flightless invertebrates such as mollusks (clams and snails), annelids (worms and leeches), and crustaceans (copepods, cladocerans, ostracods, fairy shrimp, clam shrimp, and tadpole shrimp). As wetlands dry, these organisms can bury into damp substrates to diapause, but more often produce drought-resistant eggs or cysts (that if needed can persist in dry substrates for years).
2. *Overwintering spring recruits.* These organisms can tolerate drought but have adults that emerge from the wetlands and aerially colonize new habitat, laying eggs on the water. Because water in most annual pools is only reliably present in spring, this is the season when oviposition occurs. When wetlands dry, these organisms persist as drought-resistant eggs or nymphs/larvae. Prominent examples include some Dytiscidae beetles and several Chironomidae midges. Some parasitic mites (Hydrachnidia) also fit into this group, and they disperse aerially attached to their insect prey.
3. *Overwintering summer recruits.* These organisms can tolerate drought but have adults that emerge from the wetlands and aerially colonize new habitats, laying eggs on drying wetland substrates. Because drying substrates develop in summer, this is the season when oviposition occurs. (Given the relatively minor differences with Type 2 organisms, some suggest combining Types 2 and 3). Prominent examples include some damselflies and dragonflies (Lestidae, Libellulidae), Limnephilidae caddisflies, *Aedes* and *Ochlerotatus* floodwater mosquitoes, and several Chironomidae.
4. *Non-wintering spring recruits.* These organisms cannot tolerate drought, but instead work to avoid drought. Adults aerially colonize the wetlands after they flood in spring to lay eggs. Immatures then rapidly complete development prior to seasonal drying, emerge, and migrate to other water bodies to spend the winter. Prominent examples include most water bugs (Corixidae, Notonectidae), several beetles (most Dytiscidae and Hydrophilidae beetles), Baetidae mayflies, some Chironomidae, and some dragonflies (Aeshnidae, Libellulidae). These insects mostly spend the winter in nearby aquatic habitats, but some dragonfly species (e.g., *Anax junius*) migrate to warmer areas in winter to produce another generation that then migrate back in spring to oviposit in seasonal ponds as they flood.

While devised for the invertebrate fauna in annual temporary pools of Canada, the Wiggins categories have broader utility to many kinds of nonpermanent wetlands worldwide.

Wissinger (1997) expanded on the Type 4 concept identifying invertebrates he called *cyclic colonizers*, of which some beetles (Dytiscidae) and water bugs (Corixidae) are perhaps the best examples. These organisms cycle predictably between seasonally flooded wetlands (of all kinds) and permanently flooded wetlands (or lakes or rivers). A typical scenario is for reproductive adults to leave permanent water refugia in spring to aerially colonize newly filled seasonal wetlands and lay eggs. In some cases females will then dissolve their flight muscles to provide energy and internal space for additional egg production. After ovipositing, these adults then die. The eggs hatch into a new generation of nymphs or larvae which can exploit the food-rich environments of the seasonal wetlands to develop. In some cases, these immatures develop into one or more generations of flightless short-winged adults that lack flight musculature, diverting that energy into further egg production. As the seasonal wetland begins to dry, a generation of flight-capable adults is produced which leave the site to return to permanent water refugia to spend the dry season. In the following spring, these individuals (or their progeny) then migrate back to the seasonal wetlands to begin a new cycle. Cyclic colonization permits invertebrates to effectively exploit seasonal wetlands despite lacking any ability to tolerate drying. Most cyclic colonizers are predators, and the strategy permits them to access the abundant prey that develop in seasonal wetlands soon after they fill (crustaceans, mosquito and midge larvae). Additionally, because seasonal wetlands are usually fishless, cyclic colonizers can operate there without the threat of fish predation. While migrating to and from seasonal wetlands is likely very risky, the benefits of cyclic colonization clearly outweigh the costs.

Sim et al. (2013) described how climate can influence the relative success of the four Wiggins et al. (1980) strategies. Where temporary wetlands occur in high rain areas, strong dispersers and those that require water for colonization (Types 2 and 4) are favored over weak dispersers and those that lay eggs on dry substrates. In moderately wet climates, most types of taxa can occur, although regular drying facilitates the persistence of drought-adapted taxa. Under low rainfall conditions (arid or semiarid climates), the Type 1 strategy of desiccation resistance and passive dispersal is favored because colonization from the egg bank may be more efficient than colonization via aerial dispersal. However, under extreme drought conditions, diapausing eggs or cysts of Type 1 organisms may lose viability, reducing their prevalence. Williams (1985) further elaborates on how an arid climate may affect which invertebrates exploit temporary wetlands, maintaining that Type 3 organisms that lay eggs on dry substrates may fair poorly.

Gascón et al. (2008) proposed adding a *Type 5* strategy, consisting of organisms that actively disperse between permanent and temporary water bodies via swimming or crawling, rather than aerially. Lacking desiccation resistance, they (or their progeny) must then migrate back to the source permanent habitats as the seasonally flooded habitat dries. Prominent examples include amphipod crustaceans and snails. In an analogous strategy, leptophlebiid and siphlonurid mayfly nymphs actively swim from river channels into floodplain wetlands during high water events (e.g., Galatowitsch and Batzer 2011). They complete their development on the floodplain, with nymphs often persisting in residual pools of waters long after the hydrologic connection between the river and floodplain is cut. Adult mayflies emerge from the floodplain and fly back to the river channels to lay their eggs, and the cycle repeats.

We categorized the 40 widespread macroinvertebrate taxa in Table 1.1 by whether they were desiccation resistant or instead avoided drying via migration (i.e., were Type 4 taxa sensu Wiggins et al. 1980 or cyclic colonizers sensu Wissinger 1997). Twenty-seven taxa could withstand desiccation and 23 were migratory (with ten families having both desiccation-resistant species and migratory species). While there is a considerable focus on the ability of aquatic macroinvertebrates in wetlands to tolerate drying, it is clear that migratory organisms are also very important constituents (e.g., some Chironomidae and Dytiscidae, most Ephemeroptera, Corixidae, Notonectidae, and Hydrophilidae).

Respiration Strategies of Wetland Invertebrates

The hydrology of wetlands, where shallow standing water occurs in highly organic settings, leads to inherently low levels of dissolved oxygen developing in most wetland waters. Invertebrates from wetlands have developed a particularly wide range of adaptations to acquire oxygen. The unique character of aquatic invertebrate faunas in wetlands vs. streams and rivers is largely dictated by oxygen supplies. Some aquatic insects and mollusks that thrive in well-oxygenated streams, such as Plecoptera stoneflies and non-pulmonate snails, are essentially excluded from many wetlands due to oxygen constraints.

Like invertebrates in other aquatic habitats, some wetland invertebrates still use gills (highly tracheated plates or membranes) to extract oxygen (Fig. 1.4a), including dragonflies and damselflies, mayflies, and some beetles. However, numerous wetland invertebrates rely solely on oxygen exchange across the cuticle and might seem poorly adapted for life in low-oxygen wetland waters. Some of these organisms have long tubular bodies (Fig. 1.4a, b) that yield high surface area to volume ratios to facilitate oxygen transfer (e.g., annelid worms, midge larvae); some beetle larvae (Hydrophilidae, Haliplidae) have lateral extensions of the cuticle to increase surface area. A few taxa have hemoglobin in their hemolymph (e.g., Chironomidae, Tubificidae) that serves a respiratory function (Fig. 1.4b; Resh et al. 2008). Others can switch to anaerobic respiration when oxygen supplies become too low (Mendelssohn et al. 2014).

Many aquatic invertebrates in wetlands do not extract their oxygen needs from the water, but instead directly breathe surface air. Mosquito larvae and most dytiscid beetle larvae have terminal siphons that break the water's surface to access air, often ringed with hydrophobic hairs to prevent flooding. Two genera of mosquitoes

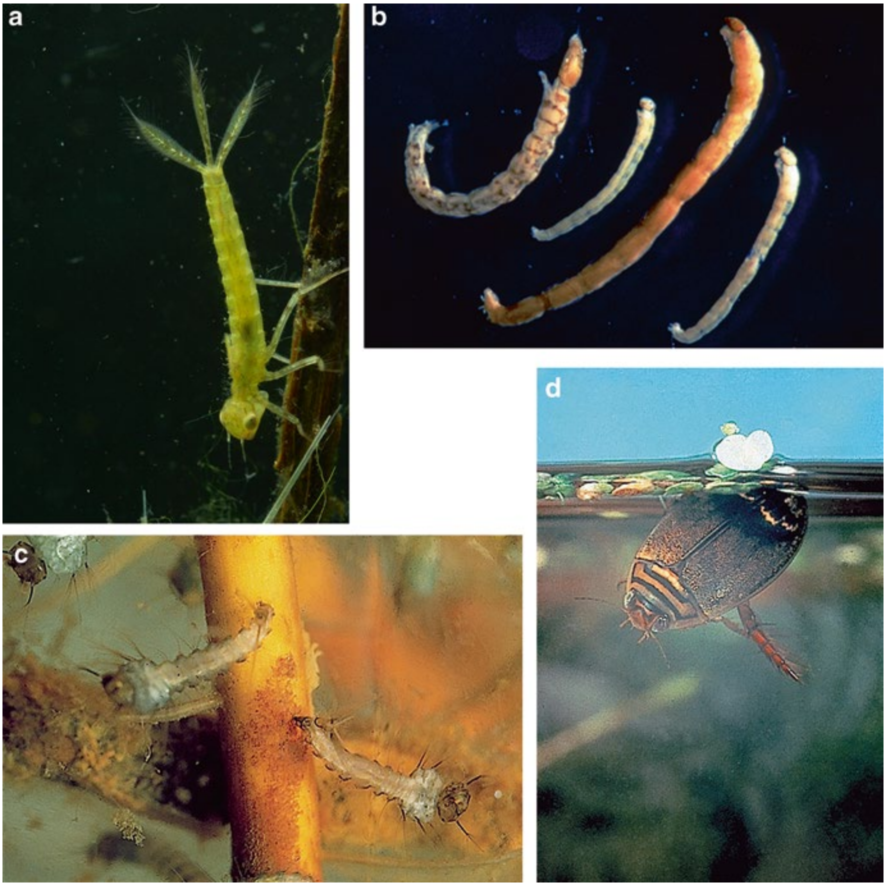

Fig. 1.4 Different adaptations of aquatic insects to extract oxygen for respiration: (**a**) damselfly nymph with three terminal gill plates on its abdomen (photo by M. Galatowitsch); (**b**) tubular chironomid midge larvae, one with reddish color from hemoglobin; (**c**) a *Coquillettidia* mosquito larvae with a siphon inserted into a plant rootlet to access internal oxygen supplies; and (**d**) a dytiscid beetle capturing an air bubble at the water's surface to place under its wings and over its respiratory spiracles. Photos **b–d** reprinted with permission from *Ecology of Freshwater and Estuarine Wetlands: Second Edition*, edited by Darold P. Batzer and Rebecca R. Sharitz. © 2014 by the Regents of the University of California. Published by the University of California Press

(*Coquillettidia*, *Mansonia*) have siphons that are adapted to pierce wetland plant roots or stems to access the air in open aerenchyma space inside the plants (Fig. 1.4c). Adult beetles and water bugs (Corixidae, Notonectidae) capture air bubbles and maintain them under their wings or along their body surfaces (Fig. 1.4d). They directly breathe the oxygen in these bubbles and also use the additional oxygen that tends to diffuse into the bubbles as internal oxygen concentrations are exhausted (this phenomenon is called the physical or compressible gill; Resh et al. 2008). Snails in wetlands are mostly pulmonates (Physidae, Planorbidae, Lymnaeidae, and

Ancylidae), derived from terrestrial ancestors and retaining air-breathing "lungs." Pulmonate snails migrate periodically to the water surface and "gulp" air into lunglike sacs to then use while underwater. Non-pulmonate snails, that dominate non-wetland freshwater habitats, have to extract their oxygen needs from water using internal gills that probably function poorly in many wetlands.

Of the 40 most widespread aquatic macroinvertebrate taxa (Table 1.1), 17 rely of surface air to satisfy their oxygen needs, 17 on respiration across the cuticle, and only 11 on gills (the total is >40 because some groups use multiple strategies). Thus, air breathing is a widely used strategy for invertebrates to exploit oxygen-poor wetland waters. However, the fact that very rudimentary cuticular respiration is also widely used by invertebrates in wetlands is perplexing and as yet unexplained.

Wetland Vegetation and Invertebrates

After hydrology, the dominant vegetation of a wetland is secondarily used for habitat categorization. Wetland floras are comprised of five main categories:

1. Emergent annual macrophytes (e.g., *Bidens*, *Polygonum*)
2. Emergent perennial macrophytes (e.g., *Carex*, *Phragmites*, *Typha*)
3. Submersed macrophytes (e.g., *Myriophyllum*, *Potamogeton*)
4. Woody trees (e.g., *Populus*, *Salix*, *Taxodium*) and shrubs (e.g., *Alnus*)
5. Algae, including cyanobacteria

Each of these plant types is controlled by hydrology. Emergent annual plants thrive in seasonal marshes and wet meadows with short hydroperiods (weeks to months), emergent perennial plants thrive in marshes with intermediate hydroperiods (months to years), and submersed plants thrive in ponds and marshes with long hydroperiods (usually multiple years). Woody vegetation in forested wetlands (often called swamps) tends to occur in short hydroperiod habitat or at least areas that are only flooded in winter and spring when trees and shrubs are largely dormant (e.g., Southeastern US floodplains). Certain wetland trees such as cypress (*Taxodium* spp.) can tolerate long-term flooding (decades), although successful reproduction requires periodic drawdown for seedlings to sprout (Schneider and Sharitz 1988). Because algae establish rapidly and can persist under all hydrologic conditions, algae tend to thrive in most wetland types, except perhaps heavily shaded forested wetlands.

Propagules of most wetland macrophytes persist in substrates as a *seed bank*, which only sprouts after the sediments are exposed during drought events. In the Prairie Pothole Region of North America (van der Valk 1981), a predictable pattern of vegetative succession occurs in response to drought with:

1. Annual plants dominating during dry phases and the early stages of reflooding
2. Perennial emergent hydrophytes dominating in subsequent years, if flooding persists

3. Eventually submersed vegetation and algae dominating with prolonged (multiple year) flooding

Euliss et al. (2004) suggest that invertebrate succession in prairie potholes will track these patterns of hydrologic and vegetative succession.

For wetland invertebrates, plants provide both habitat and food (Batzer and Wissinger 1996). Invertebrates colonize living and dead plant leaves and stems to forage and hide from predators; moist plant litter protects estivating invertebrates from excessive desiccation. Annually senescing emergent macrophytes and trees contribute copious amounts of dead leaves to wetlands, and it has long been assumed that this detritus provides the major trophic base for resident invertebrates. However, only 5 of the 40 widespread macroinvertebrates in wetlands (Table 1.1) are *shredders* (organisms that consume coarse plant matter such as dead leaves and wood). Limnephilidae caddisfly larvae are the only shredders shown to play major ecological roles in wetlands (Díaz-Villanueva and Trochine 2005; Klemmer et al. 2012, Chap. 3).

Instead, *collectors* that consume small particles of organic matter and algae comprise the bulk of the invertebrate primary consumers in wetlands (18 of 40 widespread macroinvertebrates, Table 1.1). Most food web studies in wetlands point toward algae as being the primary food base for resident invertebrates (see Batzer et al. 2014). Besides the macroinvertebrate collectors, snail *scrapers* and most microcrustaceans also feed primarily on algae. A trophic reliance by invertebrates on algae makes ecological sense because algae are an energetically superior food to macrophyte detritus (Fig. 1.5).

Predation and Wetland Invertebrates

Predation can be a pervasive influence on invertebrates in wetlands (Batzer and Wissinger 1996). Wellborn et al. (1996) argue that aquatic animal communities in lentic habitats (lakes and most wetlands) are controlled by two ecological transitions

1. Between temporary and permanent habitats (discussed above)
2. Between fish-bearing and fishless habitats

They maintained that the presence of fish in wetlands would eliminate large, active invertebrates because fish use visual cues to find prey. However, if fish were absent, these large invertebrates (along with amphibians) would become the top predators in the systems.

However, one should not assume that temporary or even ephemeral wetlands are predator-free habitats (Brendonck et al. 2002; Boix et al. 2006). Predators can be particularly important to structuring invertebrate communities of temporary wetlands because many inhabitants are poorly adapted to withstand predation

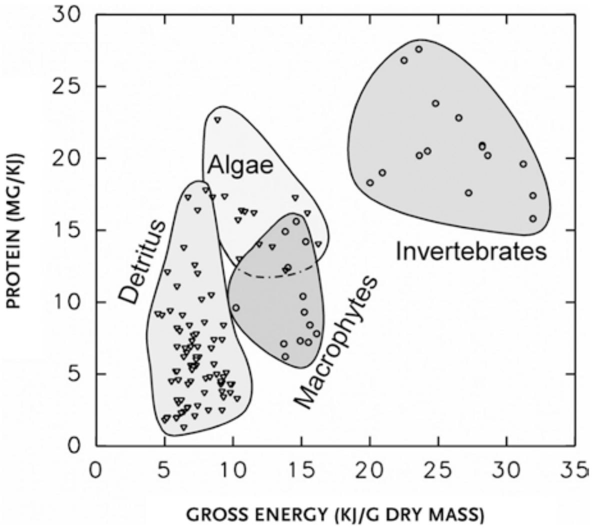

Fig. 1.5 Relative caloric and protein contents of various food resources used by invertebrates in wetlands, showing how detritus would be the lowest-quality foods and other invertebrates the highest-quality foods. Reprinted with permission from *Ecology of Freshwater and Estuarine Wetlands: Second Edition*, edited by Darold P. Batzer and Rebecca R. Sharitz. © 2014 by the Regents of the University of California. Published by the University of California Press

(Wilcox 2001; but see Petrusek et al. 2009). Aerially colonizing insects are common predators in temporary wetlands (Schneider and Frost 1996; Boix et al. 2011), and it has been shown that they can exert significant ecosystem control (Blaustein et al. 1995; Magnusson and Williams 2009).

A case for macroinvertebrate predators being ecologically important in the majority of wetlands is again bolstered by examining which taxa thrive there. In Table 1.1, 23 of 40 widespread macroinvertebrate taxa are either primary or secondary predators. Predation again makes energetic sense because invertebrate prey are high-quality foods (Fig. 1.5) (although often more energetically expensive to acquire than plants). Midge larvae, being the most widespread and typically most abundant invertebrates in wetlands (Table 1.1), are favored foods of virtually every predator that lives in wetlands, whether they be invertebrate (Rasmussen and Downing 1988; Batzer and Resh 1991), amphibian (Bohonak and Whiteman 1999; Wissinger et al. 1999), or fish (Batzer 1998; Batzer et al. 2000). The benefit of predation to invertebrates is evidenced by some limnephilid caddisfly larvae in high alpine wetlands (Chap. 3) that normally consume plant detritus (i.e., serve as shredders), but, as wetlands begin to dry, switch to being predaceous on other insects or even conspecifics in order to use the higher-quality foods to accelerate growth rates.

Importance of Wetland Invertebrates to Society

Wetlands contribute significantly to the biodiversity of the world because so many species occur solely in wetlands or at least rely heavily on wetlands to satisfy important ecological needs. While most people focus on what is often called the *charismatic megafauna*, such as the mammals, birds, reptiles, and plants of wetlands, in terms of sheer numbers of species, most of the biodiversity in many wetlands is comprised of invertebrates. It is not unusual to find more than 50 families of invertebrates in individual wetlands (see Batzer and Ruhí 2013), of which some families might be comprised of numerous genera and species. For the Chironomidae midges, the most widespread family of invertebrates in wetlands (Table 1.1), it is not unusual to find more than 50 species in an individual wetland (see Wrubleski and Rosenberg 1990; Leeper and Taylor 1998; see Chap. 10). In some cases, chironomid species richness might exceed the combined number of mammalian, avian, reptilian, and amphibian species in a wetland habitat.

Additionally, as already discussed, invertebrates play crucial roles in wetland food webs. In many cases, they are the primary trophic link between plants and the charismatic megafauna. Invertebrates feed heavily on living and dead macrophytes and algae and in turn are consumed by wetland fishes, amphibians, and birds (Fig. 1.6). Waterfowl ecologists have come to realize that most ducks consume invertebrates during crucially important periods; nesting hens rely heavily on the protein and lipids in invertebrates for egg production, newly hatched ducklings find invertebrates nutritious and easy to capture prey during their initial weeks of development, molting birds rely on invertebrates for protein for feather growth, and over-wintering migratory ducks focus on invertebrates to fuel flights back to nesting areas (see Chap. 16). Most fishes in wetlands rely on invertebrates as food (see Chaps. 8 and 10), and fishes in lakes and rivers will migrate into wetlands to consume invertebrates (see Chaps. 9, 13 and 14).

Invertebrates have proved to be useful indicators of environmental health in rivers and streams (see Rosenberg et al. 2008), and resident wetland invertebrates may show similar promise (see Chap. 15). In the wetlands of the Great Lakes of North

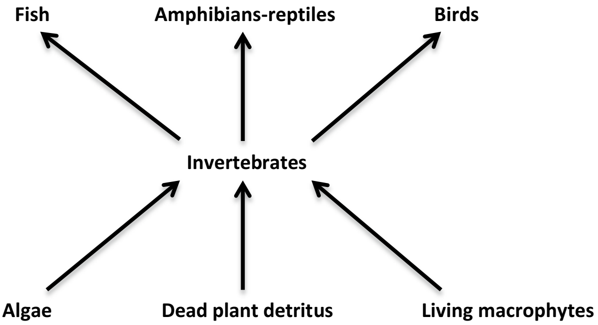

Fig. 1.6 Invertebrates as the primary trophic link between plants and higher animals in wetlands

America (see Chap. 9), invertebrates are widely used as bioindicators in habitat assessment programs. However, the fact that many invertebrates in wetlands are tolerant of harsh environmental conditions (low oxygen levels, high temperatures, fluctuating water levels) might make many taxa of fairly limited use as bioindicators (Batzer 2013). As in streams and rivers (Rosenberg et al. 2008), environmentally sensitive taxa in the insect orders Ephemeroptera, Plecoptera, and Trichoptera could be promising bioindicators in wetlands, although these organisms are not particularly wide spread in many wetlands. A recent meta-analysis suggests that the combined richness of Mollusca, Hemiptera, and Coleoptera might be a useful and easy-to-sample surrogate to predict overall invertebrate taxon richness in wetlands (Ruhí and Batzer 2014). Microcrustaceans have numerous properties that make them useful for water quality assessment (Boix et al. 2005): (a) they are ubiquitous in wetland environments and easily captured; (b) assemblages vary according to

Table 1.2 Significant human diseases associated with invertebrates from wetlands (see Mullen and Durden 2009 for more details)

Human disease	Wetland invertebrate connection
Schistosomiasis	Parasitic fluke (schistosomes) cycle between wetland snails and humans in Africa, Asia, and South America
Malaria	*Anopheles* spp. mosquitoes that breed in marshes worldwide can vector *Plasmodium* protozoan parasites
Filariasis (elephantiasis)	Various *Anopheles*, *Mansonia*, and *Culex* mosquitoes from marshes in Africa and Southeast Asia can vector *Wuchereria* or *Brugia* nematode parasites
West Nile encephalitis	*Culex* spp. mosquitoes that breed in marshes and wet meadows worldwide can vector WNE virus
Japanese encephalitis	*Culex tritaeniorhynchus* mosquitoes that breed in marshes and rice fields of Southeast Asia can vector JE virus
Eastern equine encephalomyelitis	*Culiseta melanura*, *Coquillettidia perturbans*, and *Culex* spp. mosquitoes that breed in forested swamps of the eastern USA can cycle the virus through bird populations (*Culiseta*) or vector EEE virus to humans or horses (other species)
Western equine encephalomyelitis	*Culex tarsalis* mosquitoes that breed in marshes and wet meadows of the western USA and Canada can vector the WEE virus to humans and horses
Murray Valley encephalitis	*Culex* spp. mosquitoes that breed in marshes of Australia can vector MVE virus to humans
St. Louis encephalitis	*Culex* spp. mosquitoes that breed in marshes and wet meadows of the USA can vector SLE virus to humans
Venezuelan equine encephalomyelitis	*Culex* spp. mosquitoes that breed in marshes of northern South America, Central America and Mexico, and south Florida can vector VEE virus to humans and horses
Loiasis (African eyeworm)	Tabanid deer flies that breed in damp soils and wetlands of Africa can vector the parasitic *Loa loa* nematodes to humans
Tularemia (deer fly fever)	Tabanid deer flies that breed in damp soils and wetlands of Utah and Russia can vector the bacteria
Allergies	Bites of wetland breeding mosquitoes, deer and horse flies, and biting midges (no-see-ums) can induce allergic reactions in sensitized people

differences in trophic state; (c) assemblages respond to disturbance gradients; and (d) relationships between microcrustacean assemblages and both phytoplankton and macrophyte communities are well documented. Because resident invertebrates are strongly affected by both temperature and hydroperiods, they may be especially useful bellwethers of the impacts of climate change on wetlands (Ruhí et al. 2013).

Unfortunately, some wetland invertebrates contribute significantly to human suffering. Blood-feeding mosquitoes (Culicidae), biting gnats (Ceratopogonidae), and deer and horse flies (Tabanidae) can plague humans and their livestock. Several important humans diseases, most notably malaria and schistosomiasis, are associated with invertebrates from wetlands (see Table 1.2). Because of their roles as disease vectors, it can be argued that mosquitoes are the most important animals on earth to human well-being. However, it should be noted that not all vector mosquitoes are derived from wetlands (e.g., non-wetland container-breeding species vector yellow fever and dengue viruses) and not all wetland mosquitoes are involved in disease cycles (in fact the vast majority are not).

Conclusion

Invertebrates of wetlands are uniquely adapted to exploit the highly variable and often stressful conditions that develop. Invertebrates comprise much of the biodiversity in wetlands, and invertebrates play focal roles in wetland food webs. A better understanding of the ecology of invertebrate fauna in wetlands will lead to a more complete understanding of overall wetland ecosystem functions. Toward this end, the remainder of the chapters in this book provides detailed and habitat-specific ecological information about invertebrates in wetlands from across the globe.

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