41 Ecology of Wetland Invertebrates

Synthesis and Applications for Conservation and Management

SCOTT A. WISSINGER

The purpose of this chapter is to summarize themes from the collected papers in this book and consider their importance to the overall ecology, management, and conservation of wetlands. Wetland invertebrate communities are dominated by a distinctive group of taxa, many of which do not occur in terrestrial or aquatic (>2 m depth) ecosystems. The species that dominate in wetlands can intermix with aquatic and terrestrial taxa, especially at margins, but in and of themselves most wetland communities are not ecotonal. The most often cited factor that affects species composition and diversity in wetland invertebrate communities is hydroperiod (duration, timing, and predictability of drying and filling, and permanence), and wetland invertebrates exhibit a variety of adaptations for desiccation resistance and recolonization that are effective for different types of hydroperiods. Recolonization of temporary wetlands depends on several types of dispersal between wetland basins, and the persistence of populations in one wetland depends on the presence and proximity of other wetlands and aquatic habitats. Because hydroperiod is correlated with other abiotic (dissolved oxygen, salinity, pH, nutrients, harshness of drying or freezing) and biotic (primary production, detritus breakdown, types of vertebrate predators) factors that affect invertebrates, separating the direct effects of hydroperiod from indirect effects translated through these other factors will require carefully designed manipulative experiments. Spatial heterogeneity also plays an important role in determining invertebrate community structure. Both diversity and abundance of inverte-

Invertebrates in Freshwater Wetlands of North America: Ecology and Management, Edited by Darold P. Batzer, Russell B. Rader, and Scott A. Wissinger
ISBN 0-471-29258-3 © 1999 John Wiley & Sons, Inc.

brates are higher in vegetated than in nonvegetated subhabitats, and because different taxa are associated with different plants, assemblages will be most diverse in wetlands with heterogeneous plant communities. Invertebrates play a major role in recycling nutrients and are the primary consumers through which plant production becomes accessible to higher trophic levels. Themes in this book related to the roles of invertebrates in ecosystem function include:

1. *Most below-water line macrophyte production is consumed as detritus, but herbivory on above-waterline parts of plants is probably more important than previously expected.*
2. *CPOM shredders are rare in most wetlands, and the nutrients and energy in detritus probably enter consumer webs via FPOM collectors and algal/biofilm grazers.*
3. *Benthic algae is probably more important for secondary production than previously thought in some wetlands.*
4. *Fluxes of nutrients, detritus, and organisms across wetland-aquatic and wetland-terrestrial ecotones should affect ecosystem function in wetlands and adjacent ecosystems.*

Effective conservation and management will rely on an understanding of the effects of hydroperiod and spatial heterogeneity on wetland invertebrates. Making temporary wetlands permanent will lead to changes in invertebrate species, and restored wetlands should be designed to mimic the hydroperiods in natural wetlands that perform functions comparable to those desired in restored habitats. Different species of waterfowl and other wildlife use different subhabitats that support different types of vegetation and hence different invertebrate communities; thus, basin heterogeneity (depth, substrate, hydroperiod) should be a priority for mitigation and restoration projects. Because of the importance of dispersal among wetlands, conservation strategies should account for the interdependence of different wetlands across the landscape. Finally, given their important roles in the cycling of nutrients and transformation of primary to secondary production, invertebrates should be included in functional assessment protocols for assessing the ecological integrity of natural and restored wetlands.

INTRODUCTION

Information about the ecology of wetlands has exploded during the past 25 years as ecologists, government regulators, and policy-makers have endeavored to define and delineate wetlands and to characterize their hydrologic and geomorphologic position in the landscape. The natural services that wetlands provide societies (water purification, groundwater recharge, waste processing, storm buffers, consumptive and nonconsumptive natural resources) are among the most frequently cited examples of how conservation and restoration of ecosystems can be economically beneficial (e.g., Daily 1996). Invertebrates are widely recognized as key links between wetland primary production and higher trophic levels, yet they have historically received minimal treatment in conceptual models of ecosystem function and classification. Compared to other topics such as hydrology, biogeochemistry, soils, and wetland plants, they receive minimal attention in general treatments of wetlands ecology (e.g., Good et al. 1978, Lugo et al. 1990, Mitsch and Gosselink 1993, Fretwell et al. 1996) and wetlands restoration (Kusler and Kentual 1990, Wheeler et al. 1995). Invertebrates are strikingly absent in standard methodologies for habitat integrity and functional assessment (Adamus et al. 1991, Stiehl 1994, Smith et al. 1994, Brinson and Rheinhart 1996, Wilson and Mitsch 1996) and for defining, characterizing, and delineating jurisdictional wetlands (Environmental Laboratory 1987, Sippel 1988, Federal Interagency Committee for Wetland Delineation 1989, Government of Canada 1991). Several authors in this book note that information about invertebrates is also strikingly absent in edited volumes and regional summaries of wetland ecology (e.g., Windell et al. 1986, Dammon and French 1987, Wharton et al. 1982, Myers and Ewel 1990, Epperson 1992, Playa Lake Joint Venture 1993, Davis and Ogden 1994). Much of the historical knowledge about the ecology of wetland invertebrates is based on the importance of invertebrates as food for ducks and other types of game and nongame wildlife and as biological control agents for mosquitoes (review by Batzer and Wissinger 1996, Chapters 21, 34, recent articles by Nordstrom and Ryan 1996, de Szalay et al. 1997, King and Wrubleski 1998, Turner and McCarty 1998, Safran et al. 1998). This book brings together for the first time a compilation of the current state of knowledge about the ecology of invertebrates from a wide array of wetland habitats across North America. My goal is to summarize and synthesize the major themes that emerge from this volume and extend the application of this information to include other issues of wetlands conservation and management.

WETLANDS—UNIQUE HABITATS WITH UNIQUE INVERTEBRATE SPECIES

Wetlands have often been viewed as spatial and/or temporal ecotones between water and land. However, most wetlands do not occur at the boundary between aquatic and terrestrial habitats, nor are they transitional stages in a succession from aquatic to terrestrial ecosystems (Tiner 1993; fuller explanation below). The recent shift towards viewing wetlands as unique and enduring habitats rather than as transition zones has in part been stimulated by the recognition that the dominant plants in wetlands are specialists with dis-

tributions and adaptations that are distinct from terrestrial and aquatic species. Most emergent plants are not tolerant of extended and/or deep inundation (>2 m = aquatic habitat; Cowardin et al. 1979), nor do they survive or compete well in the unsaturated, aerobic soils of terrestrial habitats. Thus, the presence of wetland plants has become one of the main criteria used for delineating wetlands for ecological and jurisdictional purposes (Tiner 1989, 1991). Below I argue that the fauna of wetlands is similarly dominated by invertebrates uniquely adapted to the shallow and often fluctuating water levels in wetlands. Rather than referring to these species as "semiaquatic"or "semiterrestrial," it would be simpler and more accurate to use the term *wetland invertebrates* to distinguish this group of taxa from those that inhabit aquatic and terrestrial habitats.

Wetland invertebrates can be distinguished from terrestrial and aquatic invertebrates at multiple taxonomic levels. Among insects and crustaceans there are entire families of wetland specialists such as marsh beetles (Helodidae), marsh-loving beetles (Limnichidae), minute bog beetles (Sphaeriidae), burrowing water beetles (Noteridae), marsh flies (Sciomyzidae), phantom crane flies (Ptychopteridae), velvet water bugs (Hebridae), water measurers (Hydrometridae), fairy shrimp (Anostraca), clam shrimp (Conchostraca), and tadpole shrimp (Nostrostraca), all of which are rarely or never encountered in aquatic or terrestrial habitats (Table 41.1). In nearly all "aquatic" families of invertebrates, specialization to wetlands has occurred at the level of subfamily, tribe, genus, and species. Some species are generalists that occur in both aquatic and wetland habitats, but in some families most species are wetland specialists (e.g., water boatmen, back-swimmers, predaceous diving beetles; Table 41.1). Several groups of "terrestrial" arthropods include families, tribes, genera, or species that occur mainly in wetlands, including a variety of plant bugs, moths, springtails, lacewings, crickets, grasshoppers, diving wasps, and spiders. Many of these taxa live on the above-water parts of wetland vegetation and are obligately associated with particular species of wetland plants as herbivores, stem borers, plant parasites, and pollinators, or are obligately associated with each other as parasitoids, predators, or commensals. Invertebrate communities in dense stands of emergent marsh vegetation (Chapters 2, 4, 15), in the trees of swamps (Chapters 5, 7, 28), in the *Sphagnum* of peatlands (Chapter 17, Rosenberg and Danks 1987), and in the phytotelm of pitcher plants (Chapters 11, 18) include many wetland specialists as well as generalist species that also occur in terrestrial habitats. Emphasizing the uniqueness of wetland taxa and their diverse taxonomic affiliations has important consequences for accurately assessing the biological diversity in wetlands (e.g., Richter et al. 1997), and for understanding the various roles that invertebrates play in wetland ecosystem function.

Wetlands often include several types of subhabitats each of which can have both above- and below-waterline invertebrate assemblages. Because many of the investigators who study wetland invertebrates have been trained as aquatic ecologists, the types of samplers, sampling strategies, and general knowledge

TABLE 41.1. Wetland Invertebrates in North America and Their Taxonomic Affinities[a]

Insects	
Bugs (Hemiptera)	1. Families in which most or all species are wetland specialists; Velvet water bugs (Hebridae), water measurers (Hydrometridae), water treaders (Mesoveliidae), pygmy back-swimmers (Pleidae), shore bugs (Ochteridae), toad bugs (Gelastocoridae), and shorebugs (Saldidae) 2. Familes of aquatic bugs with wetland specialists, aquatic specialists, and wetland-aquatic generalists; e.g., Nepidae (waterscorpions), waters striders (Gerridae), water boatmen (Corixidae), back-swimmers (Notonectidae), creeping water bugs (Naucoridae), giant water bugs (Belostomatidae)
Beetles (Coleoptera)	1. Families in which most or all species are wetland specialists; e.g., marsh bettles (Helodidae), moss beetles (Hydraenidae), minute mudbeetles (Georyssidae), burrowing water beetles (Noteridae) 2. Families with wetland and aquatic species; e.g., predaceous diving beetles (Dytiscidae), whirligig beetles (Gyrinidae), crawling water beetles (Haliplidae), water scavenger beetles (Hydrophilidae) 3. Families of mainly terrestrial beetles with wetland species; e.g., weevils (Curculionidae), leaf beetles (Chrysomelidae), rove beetles (Staphylinidae), hister beetles (Histeridae), ground beetles (Carabidae)
Flies (Diptera)	1. Families in which most or all species are wetland specialists; e.g., marsh flies (Sciomyzidae), mosquitoes (Culicidae), biting midges (Ceratopogonidae), horse and deer flies (Tabanidae), long-legged flies (Dolichopodidae), shore flies (Ephydridae) 2. Families with wetland and aquatic species; e.g., phantom midges (Chaoboridae), midges (Chironomidae), soldier flies (Stratiomyiidae), crane flies (Tipulidae), moth flies (Psychodidae), phantom crane flies (Ptychopterdae), dance flies, (Empididae), dixid midges (Dixidae) 3. Families of mainly terrestrial flies with some wetland specialists; e.g., flesh flies (Sarcophagidae), snipe flies (Rhagonidae), root maggot flies (Anthomyiidae), dung flies (Scathophagidae), small dung flies (Sphaeroceridae), rattail maggots (Syrphidae)

TABLE 41.1. (Continued)

Dragonflies (Odonata)	Families with aquatic and wetland species; e.g., common skimmers (Libellulidae), green-eyed skimmers (Corduliidae), belted skimmers (Macromiidae), darners (Aeshnidae), spread-winged damselfies (Lestidae), narrow-winged damselflies (Coenagrionidae)
Mayflies (Ephemeroptera)	Aquatic families with a few wetland species: e.g., small square-gills (Caenidae); small minnow mayflies (Baetidae), primitive minnow mayflies (Siphlonuridae), pronggills (Leptophlebiidae)
Caddisflies (Trichoptera)	Familes with aquatic and wetland species; northern case-makers (Limnephilidae), giant case-makers (Phryganeidae) long-horned case-makers (Leptoceridae)
Springtails (Collembola)	1. Families with mainly wetland species; e.g., elongate springtails (Poduridae) 2. Terrestrial families with wetland species; e.g., globular springtails (Sminthuridae, Entomobryidae)
Moths (Lepidoptera)	Terrestrial families with species having caterpillars that specialize on wetland plants; e.g., pyralid moths (Pyralidae), noctuid moths (Noctuidae), nepticulid moths (Nepticulidae), cosmopterigid moths (Cosmopterygidae), tortricid moths (Tortricidae)
Plant bugs (Homoptera)	Terrestrial families with specialists on wetland macrophytes; e.g., aphids (Aphididae), spittlebugs (Cercopidae), leafhoppers (Cicadellidae), plant hoppers (Delphacidae), sedge and grass scales (Aclerdidae)
Grasshopper and crickets (Orthoptera)	1. Families with mainly wetland species; e.g., pygmy locusts (Tetrigidae) 2. Terrestrial families with wetland species; e.g., meadow grasshoppers (Tettigoniidae), crickets (Gryllidae), grasshoppers (Acrididae)
Ants, bees, wasps (Hymenoptera)	1. Parasitic wasp families with wetland hosts; e.g., Diapriidae, Scellionidae, Ichneumonidae 2. Families with aquatic and wetland species; e.g., diving wasps (Trichogrammidae, Mymaridae)
Crustaceans	
Water fleas (Cladocera and other small branchiopods)	Many epibenthic and phytophilous species in the Daphniidae, Chydoridae, Macrothericidae, and Bosminidae occur only or mainly in wetlands.
Fairy shrimp (Anostraca)	Most species are wetland specialists.
Clam shrimp (Conconstraca)	Most species are wetland specialists.
Tadpole shrimp (Nostostroca)	Most species are wetland specialists.
Seed shrimp (Ostracoda)	Several genera and species are wetland specialists.
Copepods (Copepoda)	1. Many large calanoids are wetland specialists. 2. Many harpacticoids and cyclopoids are generalists that occur in both aquatic and wetland habitats.
Sow bugs (Isopoda)	Several species are wetland specialists and others are generalists that occur across a wide range of aquatic and wetland habitats.
Scuds (Amphipoda)	Several species are wetland specialists and others are generalists that occur across a wide range of aquatic and wetland habitats.
Crayfish, shrimp, Prawns (Decapoda)	1. Several shrimps and prawns (e.g., *Palaeomontes paludosus*) 2. Crayfish species in the family Cambaridae
Annelids	
Segmented worms	1. Many in the aquatic families Tubificidae, Naididae, Enchytraeidae 2. Many in the terrestrial family Lumbriculidae
Leeches (Hirudinea)	Temporary habitat specialists reported
Mollusca	
Snails (Gastropoda)	Species in the families Physidae, Lymnaeidae, and Planorbidae
Clams (Bivalvia)	Species in the Pisididae genera *Sphaerium, Musculium, Pisidium*
Miscellaneous Taxa	
Rotifera	Many colonial rotifers appear to be temporary wetland specialists.
Flatworms (Turbellaria)	Many restricted to temporary habitats (e.g., *Typhloplanida*).
Miscellaneous Meiofauna	Water bears (Tardigrada) and Nematoda. Common, but specialization unknown.

[a]Most taxa are listed in one or more chapters in this book. Descriptions of the particular types of habitats and microhabitats can be found in McCafferty (1983), Borror et al. (1989), Williams and Feltmate (1992), Thorp and Covich (1994), and Peckarsky et al. (1990), Merritt and Cummins (1996).

of the habits and habitats of invertebrates are biased towards collecting and studying the subset of wetland species that belong to aquatic taxa. Many authors recognize the inadequacy of coverage across all subhabitats and note that their taxonomic lists are incomplete (Chapters 7, 9, 10, 15, 21, 22, 23, 24, 28, 30, 37). Habitats that are most likely to be undersampled include dense stands of emergent vegetation, mats of floating plants, saturated soils of peatlands, fens, and wet meadows, understories and canopies of shrub thickets and wooded wetlands, and marginal habitats at wetland-terrestrial ecotones.

The spatial and temporal relationships among wetland, aquatic, and terrestrial invertebrates become most apparent when one realizes that most wetlands have, but are not themselves, ecotones (Fig. 41.1*a*). Spatially, many wetlands are surrounded completely by terrestrial habitats, and although there will be a wetland-terrestrial ecotone, the wetland itself is a unique habitat that is not adjacent to an aquatic habitat (Fig. 41.1*a*). Most wetlands described in this book are "non-ecotonal" (after Tiner 1993) (Chapters 5, 7, 8, 9, 10, 12, 13, 14, 15, 16, 19, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 34, 35, 39). In large wetland complexes ecotones can occur at the boundaries of different subhabitats, but the different subhabitats are typically not aquatic-terrestrial boundaries (Chapters 2, 4, 6, 17). The taxonomic lists in this book provide abundant evidence that the invertebrate communities in these wetlands are dominated by wetland specialists (Table 41.1) and that aquatic generalists that occur in the deepest and most permanent subhabitats are not likely to overlap in time or space with terrestrial generalists that occur at the wetland-terrestrial ecotone (Fig 41.1*a*).

Some wetlands are classic examples of ecotones in the sense that they occur between land and water; e.g., those on low-lying lake shores, in riparian zones of rivers, and adjacent to estuaries, and those associated with springs (Chapters 3, 7, 17, 20, 28, 33, 36, 37, 38, 40, Carter et al. 1994). However, many "ecotonal wetlands" (after Tiner 1993) include unique plant communities with wetland specialists that are not found in adjacent aquatic and terrestrial habitats (Fig 41.1*b*; Chapters 3, 7, 6, 37, 40, Findlay et al. 1989). Wetland invertebrates can intermix with aquatic species at aquatic-wetland ecotones and with terrestrial species at a terrestrial-wetland ecotones, but terrestrial and aquatic species do not typically overlap. Some wetland complexes will include both ecotonal and non-ecotonal habitats (Chapters 2, 4, 7, 17, 29; Naiman and Decamps 1997).

In a temporal context, wetlands have historically been viewed as transitional stages in a "hydrarch" succession in which aquatic habitats eventually fill in and become terrestrial habitats (e.g., Gates 1926). However, for most wetlands there is little botanical, geomorphological, or hydrological evidence to support this myth. Ecotonal and nonecotonal wetlands can be considered temporal ecotones in the sense that seasonal fluctuations in the water table or interannual cycles of drought are accompanied by temporal shifts in the de-

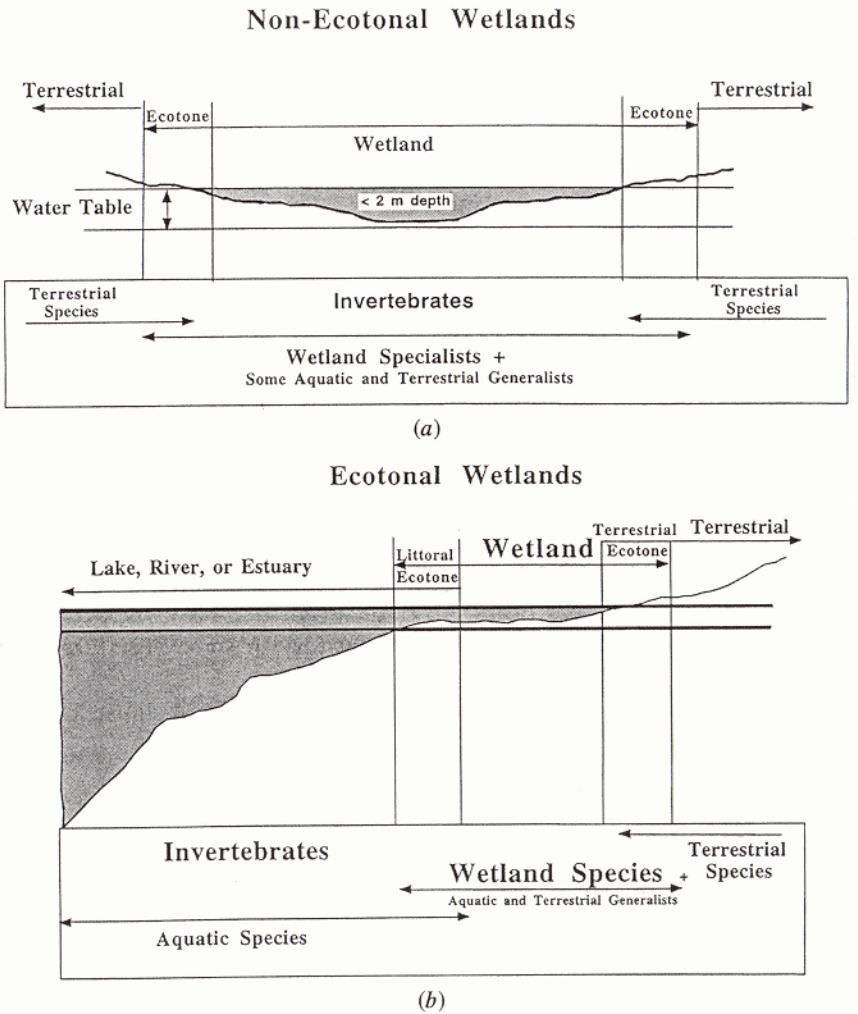

Fig. 41.1. The landscape position of (*a*) nonecotonal and (*b*) ecotonal wetlands and the distribution of wetland, aquatic, and terrestrial invertebrates (see text).

gree to which they are dominated by wetland or terrestrial plants and animals (Chapters 7, 12, 15, 17, 22, 26, van der Valk 1981, van der Valk 1978, Welling et al. 1988, Haukos and Smith 1993, Tiner 1993). However, with a few exceptions (Chapters 39, 40), wetlands exhibit cyclical patterns of change rather than linear progressions towards becoming terrestrial (Tiner 1993). In the absence of human perturbation, wetlands in North America are probably being created by natural geomorphological processes faster than they are being destroyed (Tiner 1993).

AN INVERTEBRATE-SENSITIVE PERSPECTIVE ON HYDROPERIODS

Surface water levels in most natural wetlands, even those that are permanent in most years, fluctuate seasonally, and many wetlands dry completely, either on a seasonal cycle or as a result of interannual variation in climate (i.e., drought). The schedule of filling and drying, or hydroperiod, is the most often cited form of disturbance in wetlands and is probably the single most important component of the "habitat template" (Southwood 1977, 1988). The concept of habitat template has been particularly useful to invertebrate ecologists for organizing information about tradeoffs associated with different life history and colonization strategies (reviews by Wiggins et al. 1980, Williams 1987, Batzer and Wissinger 1996, Wissinger 1997). A review of the chapters in this book suggests that a biologically relevant classification of wetland habitat templates should include the following components:

1. *Permanence* (permanent, semipermanent [dry in some years], temporary)
2. *Predictability* of drying and filling (seasonal, interannual climate cycles, relatively unpredictable)
3. *Phenology* (seasonal timing) of drying and filling
4. *Duration* of the dry and wet phases
5. *Harshness* during both phases

Several of these biologically relevant components of hydroperiod are not included in wetland classifications based on a hydrogeological perspective of wetlands (Cowardin et al. 1979, Mitsch and Gosselink 1993, Tiner 1996). Wiggins et al. (1980) distinguish temporary habitats that dry only for a short period in summer and refill in autumn ("autumnal") from those that are typically filled for only a short time in spring ("vernal"). Although some wetlands are clearly autumnal (Chapters 13, 14, 15, 19, 21, 22) or vernal (Chapter 28), many other types of temporary hydroperiods in North America reflect regional differences in climates (Fig. 41.2). For example, playas in Texas and marshes in California have a relatively short wet phase to their

hydroperiod, like vernal pools in the Northeast, but the wet phases are in the summer and winter rather than the spring and therefore might be called "summer-wet" and "winter-wet" hydroperiods, respectively (Fig. 41.2). Temporary wetlands in the Southeast are wet for most of the year, but the dry phase is at a different time of year than in autumnal wetlands of the North (Figure 41.2). I am not necessarily in favor of a proliferation in jargon, but it is not clear that these other patterns of drying and filling are any less important than autumnal and vernal patterns, and distinguishing among them is certainly biologically relevant. The duration and seasonal timing of the hydroperiod dry phase will affect invertebrate *population and community ecology*—e.g., community composition and diversity will depend on which and how many species can tolerate particular dry phases; and the roles of invertebrates in *ecosystem processes*, e.g., rates of primary production, grazing, detritus breakdown, and nutrient cycling, will all depend on which season and for how long wetlands dry (see Invertebrates and Ecosystem Function, below).

The predictability of drying and filling is a component of hydroperiod that is superimposed on permanence, phenology, and duration. Among temporary wetlands, tidal wetlands are among the most predictable (Chapters 36, 37) and those that fill only from hit-or-miss convectional storms are among the

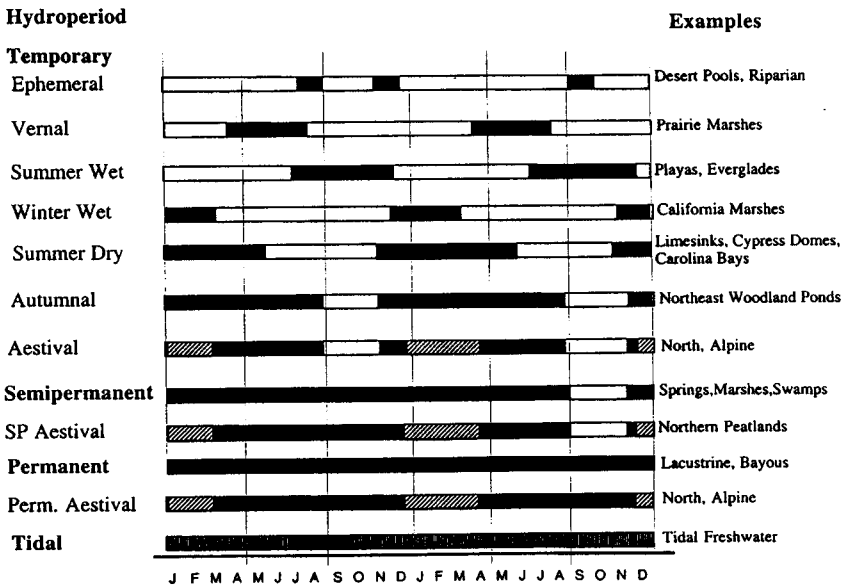

Fig. 41.2. A summary of the various hydroperiods (schedule of filling and drying) described in the chapters of this book for wetlands of North America. Differences in the degree of permanence and the duration, seasonal timing, and predictability of drying and filling can all affect invertebrate colonization strategies, community composition, and ecosystem function (see text).

least predictable (Chapter 32; Fig. 41.2). Interannual climatic variation can also create relatively unpredictable disturbances, either as drought or as extended inundation. The latter can be as important of a disturbance to invertebrate communities in temporary wetlands as drought can be to permanent habitats (Chapters 4, 5, 8; also Leslie et al. 1997, Golladay et al. 1997). Cycles of drought are perhaps best described in the Great Plains and Upper Midwest (including the Great Lakes), where wetland hydroperiods shift during droughts from permanent to autumnal and from autumnal to vernal (Chapters 21, 22, 23, 24, 38, 39). Most studies on wetland invertebrate communities are relatively short in duration, and patterns of species composition, even in "permanent" wetlands, might often reflect (unbeknownst to the investigator) differences in the time since the last extraordinary drought or inundation event associated with interannual climate variation (Chapters 15, 11, 26). Long-term studies are necessary for understanding postdrought patterns of community assembly and succession and how invertebrate communities change with cyclic changes in vegetation (Chapters 21, 22, 23, van der Valk and Davis 1978).

Temporary wetlands (Chapters 15, 22, 23, 24, 31, 32, 34), and microhabitats in them (Chapters 11, 18), are excellent model ecosystems for studying the dynamics of community assembly (e.g., Drake 1991, Lawlor and Morin 1993, Wilson and Whittaker 1995, Morin and Lawlor 1995), and for understanding the community attributes that lead to stability (resistance to and resilience after change) in communities (Tilman and Downing 1994, Naeem et al. 1994). Wetland permanence gradients provide an excellent opportunity to study the relative importance of stochastic and deterministic processes in ecological communities (Connell and Lawton 1992). In wetlands that dry frequently population dynamics and community composition should depend more on colonization dynamics than on the outcome of population interactions (competition, predation, mutualism).

Finally, the degree of harshness during both the wet and dry phase of a hydroperiod is a component of habitat templet that is often cited as having an important effect on invertebrates. Harshness during the dry phase will depend on the type of substrate, vegetation cover, and local climate. Certainly the parched, vegetation-less substrates of wetlands in relatively arid climates (Chapters 25, 26, 27, 30, 32) present different challenges for desiccation tolerance than the moist litter of woodland pools (Chapters 5, 9, 12, 14) or soils of wet meadows in humid climates (Chapters 8, 9, 13, 15). Such regional variation in harshness during the dry phase of temporary hydroperiods could underlie geographical patterns in the relative importance of different colonization strategies and the dominant species in wetland invertebrate communities (see Life History and Colonization Strategies, below). Wetlands can also vary in the degree of physical harshness during the wet phase of hydroperiods, and factors such as anoxia and freezing can affect community composition and invertebrate activities, which in turn will affect ecosystem function (Chapters 17, 18, 22, 23, 24, 25, 30, 31; Fig. 41.2).

In summary, hydroperiod classifications used for jurisdictional and definitional purposes (Tiner 1996) and functional assessments of created and restored wetlands (e.g., Brinson 1993a, b) do not provide enough information for an ecologically relevant description of wetland habitats. An invertebrate-sensitive classification scheme should include components such as predictability, timing, harshness, and duration, all of which can affect the species composition, diversity, and abundance of invertebrates and their roles in ecosystem function.

LIFE HISTORY AND COLONIZATION STRATEGIES

Given the range of disturbance regimes that can be found in wetlands (Fig. 41.1), it is not surprising that invertebrate ecologists have been interested in matching different life history and colonization strategies to particular hydroperiods (reviews by Wiggins et al. 1980, Williams 1987, Batzer and Wissinger 1996). The broad coverage of wetland types and hydroperiods in this book provides an opportunity to identify geographic and habitat-specific patterns for the importance of five basic invertebrate colonization strategies:

1. Desiccation tolerance
2. Timed emergence with adult survival in adjacent terrestrial habitat
3. Aerial dispersal from other wetland or aquatic habitats
4. Immigration and emigration in flood waters
5. Passive dispersal on other animals or by wind

There is little information on passive dispersal in this book, and our understanding of its importance continues to be constrained by the logistical difficulties of detecting it (reviews by Williams 1985, Williams and Feltmate 1992).

Desiccation Tolerance

Drying is the most important fundamental niche axis in temporary wetlands, and desiccation tolerance is perhaps the most important and defining life history characteristic of invertebrates that inhabit them (Fig. 41.2). Wetland ecologists often assume the taxa they encounter in temporary and semipermanent wetlands are able to tolerate desiccation in one or more life stages in or near dried basins (Chapters 2, 3, 4, 7, 8, 12, 13, 14, 15, 21, 22, 23, 24, 26, 28, 29, 30, 31, 32, 34, 35). Desiccation tolerance is well described for some taxa (see reviews by Wiggins et al. 1980, Williams 1987, Batzer and Wissinger 1996), but not for others, and is often only inferred from the rapid appearance of species after inundation. In many cases this inference is probably reasonable, but in others the rapid appearance of species can also be

from eggs deposited by opportunistic dispersers (e.g., chironomids), cyclic colonizers (e.g., water striders), and passive dispersers on waterbirds, all of which can arrive within a few days of inundation (references in Batzer and Wissinger 1996).

Desiccation tolerance has been especially well studied in micro- and macrocrustaceans (e.g., water fleas, copepods, fairy shrimp, clam shrimp). In some species, desiccation-tolerant eggs are known to survive several wet-dry cycles, thus forming an "egg bank" that is analogous to plant seed banks (Hairston 1995, and references in Delorme 1991, Dodson and Frey 1991, Williamson 1991). Even in permanent habitats, copepods are know to remain quiescent in the sediments for a variable number of years and time emergence seasonally to avoid fish predators (Hairston 1987, Hairston et al. 1990, 1995). The presence of egg banks in other groups of wetland invertebrates (insects, annelids, mollusks) is poorly documented, and is one challenge for future research (see Batzer and Wissinger 1996 for a few examples). A second challenge is to understand the importance of different desiccation-resistant strategies (life stage, length of diapause, hatching cues) for recolonization under different seasonal and interannual drought cycles. Although patterns of plant colonization after drought are well understood in some wetland systems (e.g., Welling et al. 1988, van der Valk and Davis 1989, Haukos and Smith 1994), comparable data are wanting for invertebrates. A third challenge for future research is to understand the relative importance of different types of substrates and refuges as sites for resisting desiccation. In addition to burrowing in sediments during drought, organisms can also be found under mats of plant detritus (Chapters 15, 34), in the stems of live or dead macrophytes (Chapters 2, 4, 15, 21, 22, 23, 38, 39), among macrophyte root masses (e.g., Chapter 34), in/under woody debris (Chapters 5, 9, 15), and in burrows of large invertebrates (e.g., crayfish, shrimp) and vertebrates (e.g., alligators, muskrats, beavers; Chapters 2, 4). We do not yet understand the relative importance of these microhabitats or whether their presence underlies interbasin differences in the composition of wetland invertebrate communities.

A fourth challenge in northern and high-elevation wetlands is to understand the importance of freezing. Winter-freeze habitats have been termed "aestival" because liquid water is not available (Welch 1952). Aestival conditions are likely in most northern and high-elevation wetlands, including those that are otherwise permanent (e.g., Chapters 12, 13, 14, 15, 17, 18, 21, 22, 23, 24, 30, 31, 32, 38, 40). Although winter mortality associated with aestival conditions (low oxygen, desiccation, physical damage from ice) is documented for particular species (e.g., Danks 1971, Daborn 1971, 1974, Daborn and Clifford 1974, Andrews and Rigler 1985), the importance of invertebrate winterkill and strategies for avoiding it have received little attention from wetlands ecologists. Between-basin differences in invertebrate community composition in northern and alpine wetland could be related to variation in tolerance to aestival conditions that has been observed among different taxa (Lee 1989, Oswood et al. 1991, Frisbee and Lee 1997). Winterkill should also play an indirect role in invertebrate community composition because it can eliminate or reduce populations of fish and amphibian predators (see Predator-Permanence Gradients, below).

The relative importance of desiccation resistance and aerial dispersal appears to depend in part on the harshness of dried substrates and in part on conditions that favor other colonization modes. A common theme in chapters that focus on wetlands in arid regions of North America is that aerial dispersal (both opportunistic and cyclic) is as important as or more important than desiccation resistance for the recolonization of temporary wetlands (Chapters 25, 27, 30, 32, 33, 34). In several studies this observation can be directly linked to the extremely harsh substrate conditions between periods of inundation (Chapters 26, 32). In contrast, desiccation resistance appears to be most important in eastern North America, where high humidities, relatively cool temperatures, and moist soils favor the survival of desiccation-tolerant life stages (Chapters 8, 9, 10, 11, 13, 14, 15). This may be especially true in wooded wetlands, where the forest canopy reduces substrate drying to the point that special adaptations for desiccation tolerance are unnecessary (Chapter 14) and at least some invertebrates can remain active long after surface water has disappeared (Chapter 7).

Timed Emergence and Recolonization by Adults

Many insects that inhabit permanent wetlands recolonize them annually from adults that emerge and then reoviposit in the same wetland. Although this is usually assumed to be the dominant mode of insect colonization in permanent wetlands, we actually know relatively little about the site fidelity of adult insects and rates of immigration and emigration (but see McPeek 1989, Michiels and Dhondt 1991). Recolonization by adult insects is also important in temporary wetlands. Many insects in temporary habitats complete development rapidly and emerge to the adult stage of the life cycle just before habitats dry (reviews by Wiggins et al. 1980, Williams 1987, Wissinger and Batzer 1986; Chapters 12, 13, 15, 31, 32). Some species deposit desiccation-resistant eggs in or near the dried basins, but others remain in the adult stage during the dry phase of the hydroperiod and deposit eggs when basins refill (Wiggins et al. 1980). Insects that are strong flyers and feed as adults (e.g., dragonflies) can remain active until basins refill (Chapter 15, Corbet 1980, Williams and Feltmate 1992). In other taxa (e.g., caddisflies, craneflies, mosquitoes) adults enter an ovarian diapause in adjacent terrestrial vegetation or soil. Temperature and photoperiod cues trigger arousal from diapause and females then oviposit (examples in Gower 1967, Wiggins 1973, Otto 1981, Pritchard 1983, Williams and Feltmate 1992, Wissinger and Brown, in press). This mode of colonization should be most important in permanent wetlands and in temporary wetlands that dry predictably and for a relatively short time (Tauber et al. 1986). For most wetlands it is difficult to assess the importance of this strategy without detailed life history information because ovipositing adults

can either be immigrants or residents. In extremely isolated, temporary habitats where immigration is unlikely, oviposition by resident adults should be the main mode of insect colonization (Chapter 33). Because this strategy relies on the presence of appropriate terrestrial habitat for feeding and/or ovarian diapause, these insects will be vulnerable to human impacts on adjacent lands. Understanding the terrestrial habitat requirements of wetland insects that spend the dry phase of hydroperiods as adults will be important for establishing criteria for terrestrial buffer zones around wetlands (e.g., Burke and Gibbons 1995).

Aerial Dispersal by Insects

Colonization by winged adult insects is an often-cited mode of wetland colonization (nearly all chapters that address colonization) that includes several different types of movements that have important consequences for understanding the genetic structure of wetland invertebrate populations and metapopulations (see Gilpin and Hanski 1991 and Hanski and Gilpin 1997). Three types of between-wetland dispersal are (1) density-dependent emigration from permanent wetlands to other habitats; (2) opportunistic colonization between temporary wetlands; and (3) cyclic colonization between permanent and temporary wetlands. Because permanent wetlands are relatively stable habitats, density-dependent emigration is a likely mechanism of population regulation, and many insects have developmental switches that trigger dispersal to other habitats in response to crowding (e.g., Denno and Grissell 1979, Denno and Roderick 1992). This type of dispersal can lead to "source-sink" population dynamics if species cannot complete development in the temporary wetlands to which they emigrate (see Pulliam 1988, Pulliam and Danielson 1988).

Opportunistic colonization is a second type of dispersal that is most likely to be important for species that colonize temporary wetlands. Opportunistic colonizers are "r-selected" species with life history characteristics that are likely to evolve when mortality is density-independent (review by Boyce 1984), as will be the case when wetlands dry rapidly and unpredictably (e.g., Chapters 12, 17, 16, 31, 32). Opportunistic colonizers can be an important component of communities in any wetland during the early stages of recolonization. Rapidly developing taxa such as mosquitoes and midges can complete development within a few weeks and escape the increasingly density-dependent conditions (competition and/or predation) created by later arriving species or the drying of extremely temporary pools (review by Batzer and Wissinger 1986). In wetlands that dry unpredictably, opportunistic colonizers can use a bet-hedging strategy that involves distributing eggs among different basins to insure that at least some propagules will survive (Chapter 32). Several authors suggest that opportunistic aerial colonizers should be most important in south temperate and subtropical wetlands in North America, where insect life histories are more likely to be multivoltine, with adult dispersers always available when habitats refill (Chapters 2, 10, 11, 28).

A third type of aerial dispersal is cyclic colonization, a strategy that involves seasonal migrations by winged adults between temporary and permanent habitats (Chapters 2, 3, 4, 8, 12, 14, 15, 17, 21, 22, 26, 31, 32, 34, 35; see review by Wissinger 1997). Although this phenomenon is well described for water bugs (water striders, water boatmen, back-swimmers; e.g., Fernando 1959, Young 1965, Landin and Vepsalainen 1977, Pajunen and Salmi 1988, Spence and Anderson 1994) and beetles (predaceous diving beetles, water scavenger beetles; see Fernando and Galbraith 1973, Landin 1976, Nilsson 1986), its importance has been largely overlooked by North American wetlands ecologists (but see Wiggins et al. 1980). Some water bugs and beetles that alternate seasonally between temporary and permanent habitats exhibit "flight polymorphisms" that involve an alternation of different types of adults that develop under different environmental conditions (reviews by Harrison 1980, Spence and Anderson 1994, Wissinger 1997). Long-winged adults in ovarian diapause typically leave permanent habitats in spring and give rise to one to several generations of highly fecund but sedentary adults (poorly developed wings or wing musculature) in temporary habitats. Long-winged adults return to permanent refuges to overwinter or when temporary habitats dry. Concurrent changes in wing morphology, reproductive state, and behavior emphasize that these developmental polymorphisms involve a suite of adaptations that are coordinated by a common set of neuro-endocrinological events. Cyclic colonizers do not necessarily exhibit wing polymorphisms, but most do exhibit seasonal or generational shifts in their allocation of resources to reproduction versus flight. Cyclic colonization should be especially important in wetland complexes with many temporary and permanent basins (Chapters 2, 4, 15, 17, 31, 32, 34, 39). Surprisingly, cyclic colonization is also documented between relatively isolated wetland basins (Chapters 8, 9, 10, 12, 13, 14, 21, 26, 28), suggesting that its importance is not limited to wetland complexes. One challenge for future research will be to quantify the degree to which the persistence of invertebrate populations in one type of wetland is dependent on the presence of other types of wetlands across the landscape (Jeffries 1994)

Colonization of Ecotonal Wetlands with Flood Waters

Invertebrates can move with the flow of water between ecotonal wetlands and adjacent aquatic habitats. In some cases riparian wetlands are population sinks for lotic species that are washed in during floods (Chapter 7), but in other cases flood-borne immigrants are important for the colonization of these habitats (Chapter 29). Some invertebrates in riparian wetlands exhibit life history strategies that involve ontogenetic habitat shifts between lotic to lentic habitats (Chapters 7, 16). This phenomenon is best described for mayflies that oviposit and complete early larval development in streams and then migrate with flood waters to wetlands where they complete development and emerge before the wetlands dry in summer (Chapters 7, 16). The movement of invertebrates

with flood and ebb tides is reported to be important in some (Chapter 37) but not in other freshwater tidal wetlands (Chapter 36). Finally, flood waters can be an important source of early colonists in wetlands that are managed as waterfowl habitat or for agriculture (Chapters 34, 35 and references therein).

COMMUNITY ECOLOGY OF WETLAND INVERTEBRATES

Correlates of Abundance and Diversity

Physiochemical factors that are most often cited in this volume as having an important influence on community composition and invertebrate abundance in wetlands include *hydroperiod* (most chapters), *dissolved oxygen* (Chapters 2, 26, 32, 37), *salinity* (Chapters 20, 21, 25, 33, 36, 37), *pH* (Chapters 4, 11, 17, 18), *suspended sediment* (Chapters 21, 27, 37), and *nutrient levels* (hypereutrophy, Chapters 2, 5, 21; hyperoligotrophy, Chapters 31, 32; dystrophy, Chapter 17). These data complement a recent review of the importance of these factors as fundamental niche constraints on the distribution and abundance of wetland invertebrates (Batzer and Wissinger 1996). In addition, two biological factors are repeatedly cited as being important to invertebrate communities in many types of wetland communities. The first is the diversity and particular species of plants in wetland basins (Chapters 2, 8, 10, 11, 14, 15, 16, 17, 18, 21, 23, 36, 37, 40), and the second is the presence or absence of fish or salamanders as top predators (Chapters 2, 8, 13, 19, 21, 24, 28, 29, 30, 31, 40).

Because hydroperiod can affect water and substrate chemistry, nutrient availability, vegetation, primary production, detritus processing, and presence of vertebrate predators, it is difficult to isolate the direct effects (drying, inundation) from the indirect effects translated through these other factors. For some factors, reasonable hypotheses can be generated for the directionality of cause and effect (Fig. 41.3). For example, hydroperiod can have a major influence on water chemistry (Mitsch and Gosselink 1993) or on the presence of top vertebrate predators such as fish and amphibians (Wellborn et al. 1996), but not vice versa. However, relationships among other factors can be reciprocal. For example, invertebrates can be affected by and affect vegetation, primary production, detritus, and nutrient availability (Fig. 41.3). My purpose here is not to attempt a synthesis of all these relationships, but simply to emphasize that there are many direct and indirect effects that wetland environments can have on invertebrates and vice versa, and it will therefore be difficult to interpret causal relationships from correlational data.

Direct and Indirect Effects of Hydroperiod on Invertebrate Communities

In many types of wetlands invertebrate diversity increases along a permanence gradient (Chapters 2, 4, 8, 12, 13, 15, 19, 20, 21, 22, 26, 31, 32, 33, 34; but

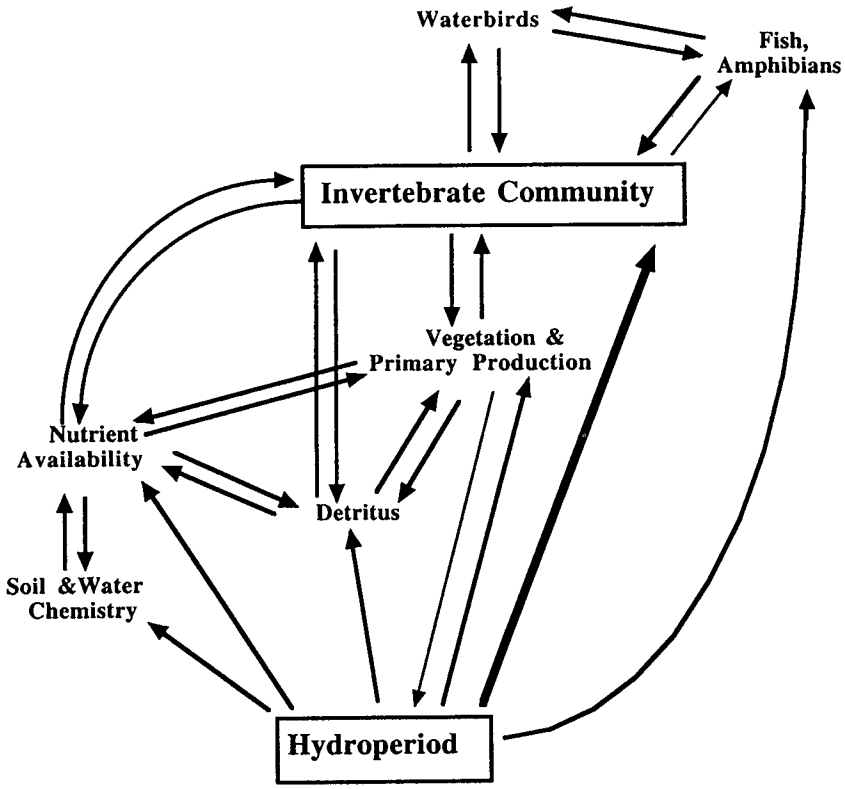

Fig. 41.3. A schematic model for the biologically relevant direct and indirect effects of hydrology on wetland invertebrates. Because many of the covariates of hydroperiod can also affect and be affected by invertebrates, it is difficult to infer the direct of effects of hydroperiod (drying) on invertebrates from comparative data.

see Chapters 5 and 9). There are several hypotheses for this observation. The most parsimonious is that many species lack adaptations for tolerating or escaping the dry phase of temporary hydroperiods. Consistent with this hypothesis is the clear permanence-diversity relationship observed in wetlands in relatively arid climates where conditions in dried basins are likely to be especially harsh (Chapters 13, 30, 31, 32). Two problems with this hypothesis are that (1) permanent-habitat species are often replaced by closely related species that are able to complete their life cycles in temporary habitats (Wellborn et al. 1996) and (2) more species are than are not desiccation tolerant in many taxa of wetland invertebrates. Two alternative hypotheses focus on the interaction between disturbance frequency and population interactions. There is experimental evidence from other ecosystems that predators become increasingly important agents of community structure along a declining gradient of disturbance. In relatively benign habitats predators are thought to be

most likely to mediate the coexistence of a diverse prey community (Chapter 13, Menge et al. 1986, Schneider and Frost 1997; but see Chesson and Huntly 1997). However, the strong correlation between the presence of top vertebrate predators and habitat permanence makes it difficult to test this hypothesis with comparative data (Predator-Permanence Gradient, below). The "intermediate disturbance hypothesis" differs in that it predicts relatively low diversity in stable habitats because competitive dominants exclude other species (e.g., lakes—see Chapter 39), and relatively low diversity in highly disturbed (temporary) habitats that contain only rapid colonizers. Semipermanent and shallow permanent wetlands that are disturbed at intermediate frequencies (occasional drought, anoxia, winterkill) should, according to this hypothesis, have the highest diversity. The observation that extended inundation in semipermanent wetlands is accompanied by a decline in invertebrate diversity (Chapters 4, 9, 21, 38, 39, 40) is consistent with this hypothesis. A fourth potential explanation is that permanent basins are on average larger than temporary basins and should therefore have more species, regardless of permanence status (references in Chapter 31; Larson and House 1990). Several mechanisms can underlie species-area correlations, including (1) a dynamic equilibrium between colonization and local extinction predicted by island-biogeography theory (MacArthur and Wilson 1967) and (2) habitat heterogeneity—that is, larger habitats contain more types of subhabitats which support different types of species. Although studies that follow changes in diversity during community assembly after drought can provide data that support one or more of the alternative explanations for diversity-permanence correlations (Chapters 13, 15, 12, 22, 23, 24, 34), separating their relative importances will require experimental manipulation of predators, temporal variability, and spatial heterogeneity in habitats of the same size (e.g., see Wilbur 1997).

Predator-Permanence Gradients

The top predators in wetland foodwebs change along permanence gradients, and these predator shifts are correlated with diversity (Chapters 2, 13), abundance (Chapters 2, 19; Mallory et al. 1994), and invertebrate community composition (Chapters 2, 4, 8, 13, 15, 19, 21, 30, 31, 40). One exception is in some floodplain wetlands where fish that colonize during floods have the same impact on invertebrates in permanent and temporary basins (Chapter 28). However, in most nonecotonal wetlands it appears there are species replacements along this predator-permanence gradient consistent with those observed in lentic aquatic habitats (Wellborn et al. 1996). The predator pattern for most non-ecotonal wetlands in North America is that:

1. Fish (e.g., centrarchid sunfish, ictalurid catfish, cyprinid minnows) are the top aquatic predators in permanent habitats that do not freeze.

2. Predatory amphibians (e.g., larvae of ambystomatid salamanders) and freeze/drought-tolerant fishes (e.g., mudminnows, green sunfish) are the top predators in permanent aestival wetlands and in temporary wetlands with a long wet-phase hydroperiod.
3. Large invertebrates (e.g., dragonfly nymphs, dytiscid beetle larvae) are the top predators in temporary wetlands with a short wet-phase hydroperiod (Chapters 2, 7, 8, 13, 15, 21, 28, 30, 31; reviews by Batzer and Wissinger 1996).

Mechanisms that underlie the shifts in top aquatic predators in wetlands include:

1. A lack of drought and freeze tolerance in most fish
2. Drying time constraining amphibian larval development (e.g., Pechman et al. 1989, Rowe and Dunson 1995)
3. The exclusion of salamanders by fish (e.g., Semlitsch 1987, Sexton et al. 1994)
4. Selective predation by fish and amphibians on conspicuous (large and/or active) invertebrate predators (reviews by Batzer and Wissinger 1996, Wellborn et al. 1996)

Most experimental data that link predator shifts with prey species-replacements along permanence gradients involve amphibians. Alternative morphologies or behaviors that are effective against different types of predators (Werner and McPeek 1994), or between traits that facilitate the timely escape from drying habitats (rapid growth) and those that facilitate coexistence with predators (e.g., Werner and Anholt 1993, Skelly 1997), are responsible for amphibian species replacements along predator-permanence gradients. The few experimental studies that causally link predator effects to invertebrate species replacements along this continuum include Dodson (1970, 1974) and Sprules (1972), who showed that size-selective predation by salamanders on zooplankton underlies differences in community composition in permanent versus temporary wetlands; McPeek (1990a, b, 1996), who demonstrated that the different species of damselflies in fish and fishless habitats exhibit antipredatory behaviors that are alternatively effective against fish and large invertebrates; and Wissinger et al. (in press), who found that caddisfly species-replacements along a predator-permanence gradient in alpine wetlands reflect a tradeoff between high activity rates for rapid development and low activity rates to facilitate coexistence with salamanders.

Although these studies explain patterns of distribution and abundance for some taxa, the generality of these results and the community-wide impacts of predation have not been separated from other hydroperiod correlates. The replacement of predator-intolerant with predator-tolerant invertebrates along

permanence gradients should in and of itself not lead to a change in diversity, suggesting that the often-observed diversity-permanence gradient is not easily explained by predator effects alone (see Direct and Indirect Effects of Hydroperiod on Invertebrate Communities, above). Understanding the cause-effect relationships of predators on wetlands invertebrate community structure will require an experimental approach that untangles predator effects from covarying hydroperiod correlates (on chemistry, nutrients, vegetation; Fig. 41.3) as well as the direct effects of hydroperiod (as in Wilbur 1997). In addition, future studies of wetland invertebrate communities should include the influence of waterfowl, wading birds, and wetland-associated songbirds as top predators on wetland invertebrates. The impacts of these predators are potentially strong, especially in small nonecotonal wetlands, where they can include both the direct effects of predation and indirect effects of waterfowl-induced changes in vegetation (Chapter 34, Batzer and Wissinger 1996).

Habitat Heterogeneity and Invertebrate Diversity and Abundance

Invertebrate diversity and abundance are often higher in vegetated than in open-bottom habitats (Chapters 2, 3, 4, 5, 10, 15, 16, 23, 24, 28, 34, 36, 37, 38; review by Batzer and Wissinger 1996 and Olson et al. 1995). The manipulation of vegetation structure is a common practice in managed wetlands and provides experimental evidence that vegetation structure is an important causal factor that affects invertebrate composition, diversity, and abundance (Chapter 34, references in Batzer and Wissinger 1996, Kirkman and Sharitz 1994, Foster and Procter 1995, de Szalay and Resh 1997). A variety of mechanisms have been offered to explain the empirical relationships between vegetation and invertebrate diversity and abundance, including that vegetation provides (1) greater surface area per se = higher densities; (2) greater surface area, hence more epiphytic biofilm for grazers = higher densities; (3) refuge from predators = higher densities (e.g., Heck and Crowder 1991, Jordan et al. 1996); and (4) more types of spatial niches = greater diversity. These explanations are not mutually exclusive, and which subset is responsible for the empirical relationship between vegetation and invertebrate abundance and diversity in appears to vary among plant species and wetland types (Batzer and Wissinger 1996). Several authors note that increased diversity and abundance of invertebrates in dense vegetation is largely due to an increase in phytophilous microcrustaceans (Chapters 38, 40).

Invertebrate diversity within wetlands also appears to be strongly affected by the number of different types of subhabitats or vegetation zones. Different types and zones of vegetation contain different invertebrate species (Chapters 2, 3, 4, 7, 8, 9, 10, 17, 19, 21, 24, 25, 34, 35), and wetlands with the greatest diversity of plant species or types of vegetation have the most diverse invertebrate faunas (Chapters 2, 4, 7, 10, 15, 16, 17, 21, 22, 23, 24, 25, 34, 35, 37, 38; also Kirkman and Sharitz 1994). Studies in which multiple sampling strategies include all vegetation zones, above- and below-water parts of emergent and floating plants, and year-round sampling have found an incredible diversity of invertebrate species (e.g., Chapter 17, Williams et al. 1994). However, most studies do not include multiple sampling strategies, all spatial habitats, and/or all hydroperiod phases or seasons, and several authors note that for one or more of these reasons their species lists are incomplete (Chapters 2, 7, 9, 15, 22, 28, 36, 37, 38; also see McElligott and Lewis 1994, Brinkman and Duffy 1996, Turner and Trexler 1997, Soumille and Thiery 1997).

In summary, it is clear that habitat heterogeneity plays a major role in determining the overall diversity of invertebrates and patterns of invertebrate distribution and abundance in a wetland. Mechanisms that underlie invertebrate-vegetation relationships are understood for some plants and some types of vegetation assemblages (review by Batzer and Wissinger 1996; also de Szalay et al. 1996), and a challenge for the future will be to broaden our understanding of the relative importance of the structural (niches, predator refuge) and trophic (as food and as a substrate for food) roles of vegetation and other sources of habitat heterogeneity in wetland ecosystems (e.g., snags and other woody debris; France 1997).

INVERTEBRATES AND ECOSYSTEM FUNCTION

Wetlands are typically autotrophic ecosystems in which primary production exceeds total community respiration. The relative importance of different primary producers (phytoplankton, herbaceous macrophytes, trees and shrubs, and/or benthic algae) varies among wetland types, but autochthonous production is usually more important than allochthonous inputs (Mitsch and Gosselink 1993; see Chapter 31 for an exception). For example, in marshes, which are among the most productive ecosystems on earth, the historical paradigm is that macrophyte production is most important and that most of this energy enters consumer foodwebs as detritus (Brisson et al. 1981; Mitsch and Gosselink 1993). Although the general tenets of ecosystem function are reasonably well understood for many wetlands (Mitsch and Gosselink 1993 and references therein), there is a paucity of detailed information about the roles that particular species or functional groups of invertebrates play in the flow of energy and cycling of nutrients in wetlands. This is somewhat surprising given the general recognition that invertebrates are the major "primary consumers" and "critical links" between primary producers and the vertebrates that are often the focus of wetlands management (waterfowl, wading birds, shore birds, fish, amphibians, mammals).

Information about the roles of different species in a foodweb is often organized by combining species into functional groups such as trophic levels or guilds. One approach is to categorize species by functional feeding groups (FFG) based on the dominant type of food consumed and their feeding mechanism (Cummins and Klug 1979, Merritt and Cummins 1996a, b, Minshall

1996). The FFG concept was developed in the context of stream ecosystems and is therefore familiar to many wetlands investigators who were trained as aquatic ecologists (e.g., Chapters 2, 3, 7, 8, 9, 10, 12, 14, 15, 16, 28, 29, 31, 34, 39, 40; also see Fredrickson and Reid 1988). Spatial and temporal variations in the abundance of different trophic groups in streams (e.g., *scrapers* of attached algae and biofilms, *shredders* of coarse particular organic matter [CPOM)], various types of *collectors* [burrowers, gatherers, filterers] of fine particulate organic matter [FPOM], and *predators*), has been important for the development of many of the current paradigms for energy flow and nutrient cycling in lotic systems (e.g., Allan 1995). Below I summarize the information presented in the various chapters in this book and/or cited in those chapters to (1) depict a general FFG model for invertebrate pathways through which primary production enters wetland foodwebs (Fig. 41.4); (2) describe patterns of spatial and temporal variation in those pathways within

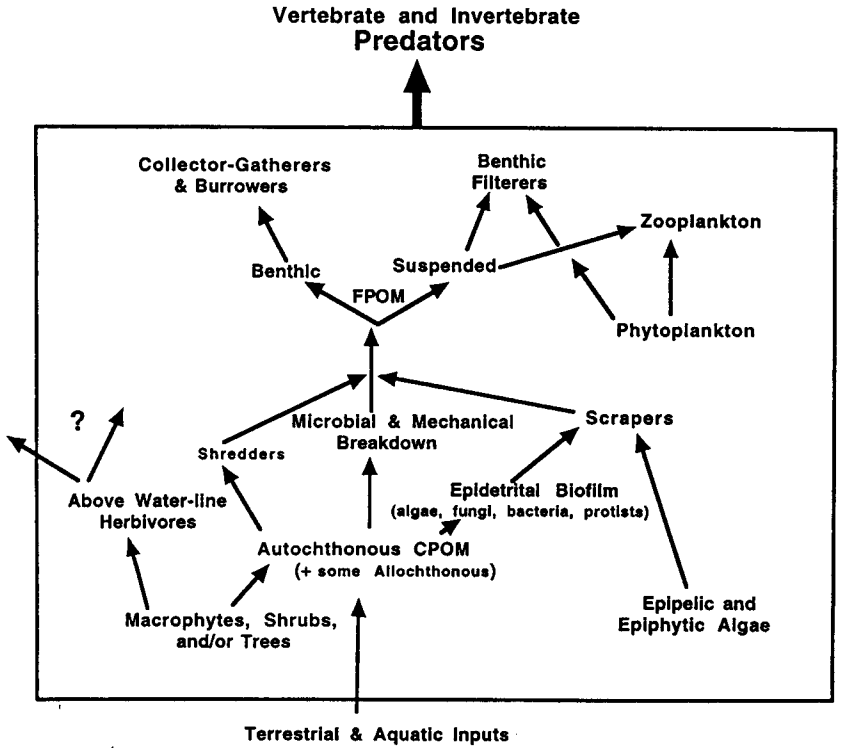

Fig. 41.4. A functional feeding group model for the various invertebrate pathways by which primary production is converted to secondary (animal) production in wetland foodwebs. The relative importance of different pathways will differ among wetlands (see Invertebrates and Ecosystem Function, above).

and among wetlands; and (3) consider areas for future research to address current contradictions and gaps in our understanding of the roles that invertebrates play in energy flow and nutrient recycling in wetlands. A caveat to this approach is that it ignores the importance of species variability and richness within these FFGs and the positive effects that redundancy can have on ecosystem stability and sustainability (Naeem 1998).

Above-Waterline Macrophyte Herbivory

In aquatic ecosystems it is generally assumed that most macrophyte production is consumed as detritus (e.g., Wetzel 1983, Jeffries and Mills 1990, Allan 1995). In wetland ecosystems this is probably true for the below-waterline parts of macrophytes (but see Feminella and Resh 1989). However, the abundance and diversity of herbivores (e.g., leaf and stem herbivores, stem borers, gall-forming insects) on the above-waterline parts of floating, emergent herbaceous, and woody vegetation suggest that live macrophyte tissue is an important invertebrate food source in many wetlands (Chapters 2, 4, 7, 10, 15, 17, 21, 22, 23, 24, 30, 38). Several studies have quantified the importance of the various types of herbivores that occur in the canopy of dense stand of emergent macrophytes (review by Batzer and Wissinger 1996), but there is little information about the importance of this herbivory in terms of energy flow and nutrient movement (Fig. 41.4). Similarly, few studies have quantified the importance of herbivory in the canopies of trees and its ecosystem consequences, including the potential for the fallout of frass and feces into the water and the effects of defoliation on light penetration (Goyer et al. 1990). Clearly one challenge for the future is to quantify above-ground herbivory and the degree to which nutrients and energy are returned to the below-waterline foodweb or exported to adjacent habitats (Fig. 41.4).

Relative Importance of Algal and Macrophyte Production

The relative importance of macrophyte detritus versus benthic algae for invertebrate production appears to vary considerably among wetland types. Leaves and wood are certainly important food sources in forested wetlands (Chapters 5, 9, 12, 14, 28) where invertebrate communities are dominated by CPOM detritivores, especially micro- and macrocrustaceans (isopods, amphipods). In some marshes invertebrate production is also thought to be driven mainly by the abundance of macrophyte detritus, but in marshes, it is insects that are typically the major detritivores (Chapters 15, 16, 17, 31). In some marshes, there is evidence that benthic algae are far more important than previously suspected. For example, the use of stable isotopes of carbon and nitrogen has revealed that much of the energy entering consumer foodwebs is from benthic algae rather than macrophytes (Goldsborough and Robinson 1996, Robinson et al. 1997a, b). Isotopic signatures suggest that in some wetlands epiphytic and epidetrital algae is more important to invertebrate

grazers than mats of filamentous algae (Chapters 4, 21; but see Chapter 30). Algal blooms that occur after reinundation in temporary wetlands are thought to be especially important for the remobilization of nutrients mineralized during the dry phase of the hydroperiod (Chapters 2, 3, 4, 21, 23, 24, 34; references in Batzer and Wissinger 1996). Clearly there is a need for future research to determine the relative importance of algal and macrophyte production across different types of marsh habitats and at different times during hydroperiods (Chapters 2, 4, 10, 19, 25, 28, 34, 36, 38, 39).

Detritus Processing by Invertebrates in Wetlands

There is an obvious paucity of shredders in many wetland invertebrate communities, even in wetlands with dense stands of macrophytes (Chapters 10, 12, 21, 22, 23, 24, 37, 40; but see Chapter 2). This is curious because the general paradigm for the breakdown of vascular plant detritus is that (1) soluble constituents leach as dissolved organic matter; (2) microbes (first fungi and then bacteria) "condition" CPOM by breaking down refractory constituents (cellulose, hemicellulose, lignin, etc.) and incorporating dissolved nutrients (especially nitrogen and phosphorus); (3) shredders then consume this conditioned CPOM-microbial complex; and (4) this shredding produces both local and exported sources of food that is then available for a variety of FPOM collectors (gatherers, burrowers, filterers) (Anderson and Sedell 1979, Barlocher and Kendrick 1985, Cummins et al. 1989, Webster and Benfield 1986, Allan 1995).

There are several potential explanations for the dearth of shredders in vegetated wetlands. First, in northern wetlands some dominant shredders (e.g., limnephilid caddisflies) have life cycles timed such that larvae hatch in autumn when macrophyte CPOM is at a maximum. Larvae are present only from late autumn to early spring, when sampling is least likely. Although this might explain the underrepresentation of shredders in northern wetlands (12, 13, 14, 15, 17, 21, 22, 23, 24, 40), it does not provide a general explanation for low shredder diversity and abundance in other wetlands. A second potential explanation is that low oxygen levels in the detritus inhibit microbial conditioning and/or shredder colonization, which should lead to the accumulation of organic matter. While organic matter does accumulate in some ombrotrophic wetlands, it does not in other types of wetlands that also lack shredders. For example, many ecotonal wetlands are open to adjacent aquatic systems and presumably better oxygenated (Mitsch and Gosselink 1993). Export to adjacent aquatic habitats is one potential explanation for the absence of both shredders and accumulated organic matter (Chapters 3, 7, 16, 29, 33, 36, 37, 38, 40). Organic matter accumulation is less likely in temporary than in permanent wetlands because detritus can be mineralized during the dry phase of the hydroperiod. Algal blooms occurring after reinundation are thought to be stimulated by the abundance of nutrients released during dry-phase mineralization of macrophyte detritus (Chapters 2, 3, 4, 21, 23, 24, 34; also Batzer and Wissinger 1996). Macrophytes are still the ultimate primary source of the energy and nutrients, but the pathway by which the nutrients enter the consumer web is through grazers on benthic algae rather than through the CPOM shredder-FPOM collector pathway (Fig. 41.4).

A third explanation for the paucity of shredders in many wetlands is that the rapid breakdown of herbaceous plant material by mechanical, microbial, and chemical processes precludes shredding. This would be especially true for submergent and floating plants with short half-life decay rates (review by Webster and Benfield 1986; also Chapters 21, 23, Findley et al. 1990). Annual plants that rapidly invade dried basins might also produce an abundance of fast-decaying detritus that, upon inundation, should support dense populations of grazers and FPOM collectors, especially chironomid midges (Chapter 24). The importance of this detritus as a basis of secondary production is no less important than if they had been eaten by shredders, but the energy and nutrients enter the consumer web via a different route than that suggested by the shredder paradigm (Fig. 41.4). One route could be epidetrital biofilms, which are important substrates for both scrapers and epibenthic microcrustaceans in wetlands. Relatively little is known about the movements of nutrients and energy from macrophyte detritus to the autotrophic (algae, protists), heterotrophic (bacteria, fungi) and nonliving (trapped FPOM, extracellular microbial matrices) components of attached biofilms. The importance of algae and other biofilm constituents as a trophic basis for secondary production in wetlands could be tightly linked to this alternative pathway for detritus mineralization.

Energy and Nutrient Fluxes across Wetland Ecotones

Spatial subsidies of energy across ecosystem boundaries can have important effects on foodweb dynamics (review by Polis et al. 1997). Invertebrates can play various roles in the flux of energy and nutrients across both terrestrial-wetland and aquatic-wetland ecotones (Fig. 41.1). Several authors have suggested that invertebrates in open, ecotonal wetlands (e.g., Chapters 3, 7, 16, 29, 33, 36, 37, 38, 39) are less likely to be food-limited than those in non-ecotonal wetlands. Historically, invertebrates in riparian wetlands (including freshwater tidal wetlands) have been considered to be of fundamental importance for the modification, storage, and transfer of dissolved and particulate organic matter en route from terrestrial and wetland ecosystems to stream channels (e.g., Odum 1988, Cummins et al. 1989, Allan 1995; Naiman and Decamps 1997). More recently, the movement of the invertebrates themselves (both aerially and in flood and ebb water) has been identified as having potentially important impacts on the energy budgets of both the wetland and adjacent aquatic ecosystem (e.g., Chapters 7, 16, 37). Although these links are generally assumed to be important, there is little quantitative evidence for how such spatial subsidies influence ecosystem function in ecotonal wetlands (Odum 1988).

It is generally assumed that both the energy and the nutrients in aquatic and aerial stages of invertebrates that are consumed by birds, mammals, and amphibians are transferred to adjacent terrestrial habitats, but the energetic importance for either ecosystem has not been documented (Batzer and Wissinger 1996). It is perhaps not surprising that freshwater wetlands have yet to play a major role in the development of general models for the importance of spatial subsidies to foodweb dynamics (Polis et al. 1996, 1997).

Integrating Community and Ecosystem Ecology—The Trophic Basis of Production

Clearly there is still much to learn about the roles that invertebrates play in the movements of energy and nutrients within wetlands and between different wetland subhabitats and adjacent ecosystems. The use of stable isotopes will play an important role in testing various hypotheses about the relative importance of different trophic pathways and the relative importance of different energy sources for consumer foodwebs in wetland ecosystems (general reviews by Peterson and Fry 1987, Fry 1991, Lajtha and Michener 1994). Constructing functional foodwebs requires population and community data about which species interact (connectivity webs) and quantitative information about the sources and amounts of energy transferred across links (Paine 1992). One approach is to quantify rates at which different sources of primary production are transformed to secondary production (as in Benke and Wallace 1997 and references therein). Understanding the trophic basis of invertebrate production in wetland foodwebs will be important for interpreting experiments designed to determine the degree to which primary production in wetlands is controlled by top-down (the cascading effects of predator removal/addition at the tops of foodwebs) versus bottom-up processes (nutrient limitation) (Batzer and Resh 1991, Batzer 1998).

APPLICATIONS FOR CONSERVATION AND MANAGEMENT

Wetlands are threatened by various human activities, and these threats and the effects on wetland invertebrates are reviewed in nearly every chapter in this book. Other applied issues that are addressed in individual chapters include:

1. The roles that invertebrates play in the conservation and management of waterfowl and other wildlife such as shorebirds, songbirds, and amphibians (Chapters 2, 10, 21, 22, 23, 24, 25, 26, 28, 30, 31, 34, 35, 36, 37, 38, 39, 40)
2. The role of invertebrates for pest control management, especially mosquitoes and invasive alien plants (Chapters 28, 34, 35)

3. The conservation of invertebrate biodiversity in wetlands (Chapters 8, 11, 13, 17, 18, 21, 26, 30, 33)
4. Invertebrates as bioindicators of ecosystem health (Chapters 2, 3)
5. Recommendations for encouraging the development of invertebrate communities in restored (Chapters 3, 4, 5, 15) and created wetlands (Chapter 4, 5, 19)
6. The effects of land use impacts on adjacent aquatic and terrestrial ecosystems (Chapters 3, 7, 12, 16, 28, 29, 36, 37, 38, 39)
7. The interdependency of wetlands linked by dispersal (Chapters 14, 15, 21, 26, 31)

The importance of wetland invertebrates has long been appreciated by those interested in wetland habitats for the conservation and management of waterfowl and for controlling pests (Eldridge 1990), and much of the rapidly growing literature on this subject is referenced in the individual chapters listed above and in Batzer and Wissinger (1996). Below I will focus on the application of the information in this synthesis to wetlands regulations, for rationales and strategies for conservation, and for the design of constructed (created, restored, enhanced) wetland habitats.

Protecting Wetlands as Enduring Habitats with Unique Species

Conceptualizing wetlands and wetland plant and animal communities as unique and enduring features of the landscape has important ramifications for conservation and management. The message that most wetlands are not transient stages in an aquatic to terrestrial succession (So why not just fill them in now!) and not just boundaries between terrestrial and aquatic habitats is a particularly important one for wetland ecologists to impart to regulators, policy-makers, and the public. The recognition of the uniqueness of wetland invertebrate communities (Table 41.1) has lagged behind a similar recognition for wetland plant communities. Just as hydrophytic plants have been classified (obligate wetland, facultative wetland, facultative, facultative upland) for recognizing and delineating wetlands (Tiner 1991, 1993a, b), so too could invertebrates and invertebrate communities be used for determining boundaries between wetland and upland habitats. Such corroborative evidence would be especially useful along relatively flat gradients where delineations based on the three primary indicators can be difficult (see Tiner 1993, Davis et al. 1996).

Also to be emphasized in distinguishing wetland from aquatic and terrestrial invertebrates is that the destruction of wetlands will lead to the local extinction of these species. Most wetland species cannot just move to terrestrial or aquatic habitats when wetlands are filled or excavated. Invertebrate biodiversity typically exceeds that of wetland plants and vertebrates combined, and pointing out that the loss of wetland habitats will lead to the loss

of invertebrate species is an under-appreciated rationale for the preservation and conservation of wetland habitats (Foster and Procter 1995). The loss of wetlands will also affect terrestrial organisms that depend on them as local concentrations of food (Gibbs 1993, Turner and McCarty 1997).

Changing the Hydroperiods of Natural Wetlands

There is an abundance of evidence that wetlands with different hydroperiods contain distinctly different invertebrate communities that are either directly or indirectly dependent on particular temporal patterns of drying (or not) and refilling (see Direct and Indirect Effects of Hydroperiod, above). Temporary wetlands in particular have disappeared at an alarming rate because these shallow basins and depressions are (1) sensitive to changes in the water table associated with human activities; (2) easily drained, filled, and/or converted to agricultural land (Chapters 3, 8, 9, 17, 21, 25, 26, 35); and (3) often excavated and deepened into permanent aquatic habitats for recreation (Chapters 2, 3, 8, 21, 27, 37; also Tiner 1984, Abernathy and Turner 1987, Dahl 1990, Cashin et al. 1992, Fretwell et al. 1996). Converting wetlands to deep-water habitats (>2 m) will result in the replacement of temporary with permanent wetland species, which in turn can affect waterfowl and other wildlife dependent on particular species, types, and sizes of invertebrates (Chapters 4, 5, 8, 21, 34, Batzer and Wissinger 1996, Collinson et al. 1995). Making wetlands permanent will also reduce invertebrate abundances as a result of fish predation (e.g., Chapters 2, 19, Hanson and Butler 1994, Mallory et al. 1994). In terms of ecosystem function, the importance of seasonal drying for the remobilization of nutrients and subsequent flushes of invertebrates after inundation is a well-known phenomenon that is an important component of waterfowl conservation and management (Chapters 21, 22, 23, 24, 28, 34, Fredrickson 1991). Although some state laws regulate the conversion of wetlands to deep-water habitats, federal wetland laws do not. They also do not give regulators jurisdictional powers related to changes in adjacent land use, buffer zones, alterations to waterways, or withdrawals from local aquifers, which can all lead to changes in the hydroperiods of natural wetland basins (e.g., Richardson and McCarthy 1994, Findlay and Houlahan 1997). The information presented in this book makes it abundantly clear that wetland invertebrate communities are not all alike and that particular assemblages of wetland animals will be associated with particular wetland hydroperiods.

Constructing Wetlands—Temporal Variability and Spatial Heterogeneity

Although constructed wetlands have been increasingly used to mitigate for jurisdictional encroachments into natural habitats, few are monitored after construction to assess the degree to which they mimic the natural wetlands they were intended to replace (review by Bedford 1996; Mitsch and Wilson 1996). When follow-up studies have been conducted on mitigation projects, the most important problems have been related to hydroperiod, and in particular to depth and to making habitats permanent (e.g., Erwin 1991, Confer and Niering 1992). Many of the chapters in this book provide evidence that permanent constructed habitats will not contain the same invertebrate communities, support the same types of game and nongame wildlife, or function in the same ways as the natural temporary habitats that they were intended to replace. There is increasing interest in the development of standards for evaluating the degree to which mitigation wetlands act as functional replacements for the impacted sites they are designed to replace (Smith et al. 1994, Brinson and Rheinhardt 1996, Wilson and Mitsch 1996). Unfortunately, neither the reference standards that are being developed nor the assessment tools that have historically been used to evaluate the functional integrity of wetlands (e.g., wetland evaluation technique = WET, Adamus et al. 1991; habitat evaluation procedure = HEP, Stiehl 1994) rely on any information about wetland invertebrate communities or their role in ecosystem function. Some restoration efforts are sensitive to the importance of hydroperiod. For example, wetlands constructed by the U.S. Fish and Wildlife Service's Partners for Wildlife Program are designed to restore wetland habitats that previously drained for agriculture (Brown 1994). A primary objective of this program is to restore waterfowl habitat and the basins are designed to be shallow and to fluctuate seasonally with groundwater levels or via manipulation with control structures (as in Reid and Fredrickson, 1988, Fredrickson 1991, Chapter 34 and references therein).

A second theme in this book is the importance of spatial heterogeneity, and in particular vegetation as habitat and food or food substrate. The different types of invertebrate communities that develop in different wetland microhabitats attract different species of birds, which require different types and sizes of invertebrate prey and different habitat types and depths for efficiently exploiting those prey (divers, dabblers, waders, etc.). Thus, wetlands should be constructed with subhabitats that differ in hydroperiod, depth, and types of substrates to support a greater diversity of plants, hence invertebrates, and hence wildlife, than those with one homogeneous basin (Chapters 15, 21, 24, 26, 28, and 34 and recent articles by Grover and Baldassarre 1995, Galatowitsch and van der Valk 1996, VanRees-Siewert and Dinsmore 1996, Turner and McCarty 1997). Habitat heterogeneity is easily quantifiable and could easily be incorporated into functional assessment protocols as an indicator of invertebrate diversity (as in Brinson and Rheinhardt 1996).

Metapopulations of Wetland Invertebrates and Landscape Management

A second level of habitat heterogeneity that is important for the establishment and persistence of diverse invertebrate communities is related to the landscape position of wetlands with respect to each other and to adjacent terrestrial and/or aquatic habitats. Because some wetland insects that live in temporary

habitats use adjacent terrestrial habitats as sites for adult diapause or feeding during the dry phase of the hydroperiod, buffer zones of native vegetation will be important for the maintenance of those wetland communities (see Timed Emergence and Recolonization by Adults, above). Current federal and state/provincial regulations that protect wetlands often do not prescribe buffer zones widths based on any knowledge of their importance to the animals that live in those wetlands (Findlay and Houlahan 1997, but see Brown et al. 1990). Invertebrate communities in ecotonal wetlands depend on movements of organisms across the wetland-aquatic ecotone, and those fluxes depend on natural hydrologic fluctuations (tides, seiches, floods) and on the geomorphologic integrity of the landscape (Chapters 3, 7, 16, 28, 29, 36, 37, 38, 40; also see O'Neill et al. 1997).

Dispersal by opportunists and cyclic colonizers is an important source of colonists in all wetland communities. Discrete populations and communities that are connected by dispersal are likely to function as metapopulations and even metacommunities (see introduction by Hanski and Simberloff 1997). Theoretical and empirical studies of metapopulations suggest that the removal of one or more habitats (subpopulations) will affect whether other subpopulations or the entire metapopulation will persist (see reviews by Gilpin and Hanski 1991, Hanski and Gilpin 1997). Even small satellite populations can be important for the long-term persistence of metapopulations (Doak and Mills 1994). Because wetlands are often discrete habitats embedded in terrestrial landscapes, effective conservation and restoration strategies are especially likely to depend on an understanding of how the persistence of viable populations in one habitat depend on the proximity to other wetlands and particular types of wetlands (Jeffries 1994, Harrison and Fahrig 1995, Moloney and Levin 1996, Bell et al. 1997).

Species Diversity and Ecosystem Functions and Services

Two themes that have emerged from this book are that (1) many interacting factors can affect community composition and diversity in wetlands (Fig. 41.1); and (2) there are many gaps in our knowledge about the relative importance of different functional groups and pathways by which invertebrates process primary production and how that varies among wetland types and across hydroperiod gradients (Fig. 41.3). Lumping taxa into functional groups is useful for structuring our thinking about ecosystem function and simplifying the taxonomic resolution that is necessary for assessing ecosystem health (e.g., Chapter 3; also Korner 1993, Gitay et al. 1996). However, biomonitoring approaches that lump species by functional groups ignore the importance of species richness within these groups. Historically the term *species redundancy* has had a negative connotation among conservation biologists because it has been used to imply that some species within a functional group might be superfluous. However, there has been a recent flurry of research that empirically links biodiversity to ecosystem stability (resistance to perturbation and resilience after perturbation) and to the sustainability and reliability of ecosystem function (material cycling and energy flow) (Tilman 1994, Naeem et al. 1995, Tilman et al. 1996, McGrady-Steed et al. 1997, Naeem and Li 1997, Naeem 1998). Because invertebrates are the primary consumers of plant production in wetlands, diversity within functional groups (i.e., species redundancy) could be necessary for the reliability of ecosystem function and hence the ecosystem services that wetlands provide societies.

ACKNOWLEDGMENTS

Comments by Darold Batzer and Russ Radar greatly improved the manuscript. Thanks to Sue and AJ for their patience. I gratefully acknowledge the support of the National Science Foundation (DEB-9407856).

LITERATURE CITED

Abernathy, Y., and R. E. Turner. 1987. U.S. Forested Wetlands: 1940–1980. Bioscience 37:721–727.

Adamus, P. R., L. T. Stockwell, E. J. Clairain, M. E. Morrow, L. P. Rozas, and R. D. Smith. 1991. Wetland Evaluation Technique (WET). Vol. I. Literature Review and Evaluation Rationale. Technical Report WRP-DE-2. U.S. Army Corps of Engineers Waterways Experiments Station, Vicksburg, MS.

Allan, J. D. 1995. Stream Ecology: Structure and Function of Running Water. Chapman & Hall, New York.

Anderson, H. H., and J. R. Sedell. 1979. Detritus processing by macroinvertebrates in stream ecosystems. Annual Review of Entomology 24:351–377.

Andrews, D. A., and F. H. Rigler. 1985. The effects of an Arctic winter on benthic invertebrates in the littoral zone of Char Lake, Northwest Territories. Canadian Journal of Zoology 63:2825–2834.

Barlocher, F., and B. Kendrick. 1985. Leaf-conditioning by micro-organisms. Oecologia 20:359–362.

Batzer, D. P. 1998. Trophic interactions among detritus, benthic midges, and predatory fish in a freshwater marsh. Ecology 79:1688–1698.

Batzer, D. P., and V. H. Resh. 1991. Trophic interactions among a beetle predator, a chironomid grazer, and periphyton in a seasonal wetland. Oikos 60:251–257.

Batzer, D. P., and S. A. Wissinger. 1996. Ecology of insect communities in nontidal wetlands. Annual Review of Entomology 41:75–100.

Bedford, B. L. 1996. The need to define hydrological equivalence at the landscape scale for freshwater wetland mitigation. Ecological Applications 6:57–68.

Bell, S. S., M. S. Fonseca, and L. B. Mooten. 1997. Linking restoration and landscape ecology. Restoration Ecology 5:318–323.

Benke, A. C., and J. B. Wallace. 1997. Trophic basis of production among riverine caddisflies: Implications for food web analysis. Ecology 78:1132–1145.

Boyce, M. S. 1984. Restitution of r- and K-selection as a model of density-dependent model natural selection. Annual Review Ecology Systematics 15:427–449.

Brinkman, M. A., and W. G. Duffy. 1996. Evaluation of four wetland aquatic invertebrate samplers and four sample sorting methods. Journal of Freshwater Ecology 11:193–200.

Brinson, M. M. 1993a. A Hydrogeomorphic Classification for Wetlands. Wetland Research Program Technical Report WRP-DE-4. U.S. Corps of Engineers Waterways Experiment Station, Vicksburg, MS.

———. 1993b. Changes in the functioning of wetlands along environmental gradients. Wetlands. 12:65–74.

Brinson, M. M., and R. Rheinhardt. 1996. The role of reference wetlands in functional assessment and mitigation. Ecological Applications 6:69–76.

Brisson, M. M., A. E. Logo, and S. Brown. 1981. Primary productivity, decomposition, and consumer activity in freshwater wetlands. Annual Review of Ecology and Systematics 12:123–161.

Brown, D. F. 1994. A partnership for wildlife. Pennsylvania Game News 65:28–32.

Brown, M. T., J. M. Schaefer, and K. H. Brandt. 1990. Buffer Zones for Water, Wetlands, and Wildlife in East Central Florida. Final Report, Florida Agricultural Experimental Station, Center for Wetlands, University of Florida, Gainesville, FL.

Burke, V. J., and J. W. Gibbons. 1995. Terrestrial buffer zones and wetland conservation: A case study of freshwater turtles in a Carolina Bay. Conservation Biology 9:1365–1369.

Carter, V., and P. T. Gammon, and M. K. Garrett. 1994. Ecotone dynamics and boundary determination in the Great Dismal Swamp. Ecological Applications 4:189–203.

Cashin, G. E., J. R. Dorney, and C. J. Richardson. 1992. Wetland alteration trends on the North Carolina coast. Wetlands 12:63–71.

Chesson, P., and N. Huntly. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. American Naturalist 150:519–533.

Collinson, N. H., J. Bigg, A. Corfield, M. J. Hodson, D. Walker, M. Whitfield, and P. J. Williams. 1995. Temporary and permanent ponds: An assessment of the effects of drying out on the conservation value of aquatic macroinvertebrate communities. Biological Conservation 74:125–133.

Confer, S. R., and W. A. Niering. 1992. Comparison of created and natural freshwater emergent wetlands in Connecticut. Wetlands Ecology and Management 2:429–447.

Cornell, H. V., and J. H. Lawton. 1992. Species interactions, local and regional processes, and limits to the richness of ecological communities: A theoretical perspective. Journal of Animal Ecology 61:1–12.

Corbet, P. S. 1980. Biology of Odonata. Annual Review of Entomology 25:189–210.

Cowardin, L. M., V. Carter, G. C. Gloet, and E. T. LaRoe. 1979. Classification of Wetlands and Deepwater Habitats of the United States. U.S. Fish and Wildlife Service Report FWS/OBS-79-31.

Cummins, K. W., and M. J. Klug. 1979. Feeding ecology of stream invertebrates. Annual Review of Ecology and Systematics 10:147–172.

Cummins, K. W., M. A. Wilzbach, D. M. Gates, J. B. Perry, and W. B. Taliaferro. 1989. Shredders and riparian vegetation. Bioscience 39:24–30.

Daborn, G. R. 1971. Survival and mortality of coenagrionid nymphs (Odonata: Zygoptera) from the ice of an aestival pond. Canadian Journal of Zoology 57:2143–2152.

———. 1974. Biological features of an aestival pond in western Canada. Hydrobiologia 44:287–299

Daborn, G. R., and H. F. Clifford. 1974. Physical and chemical features of an aestival pond in western Canada. Hydrobiologia 44:43–59.

Dahl, T. W. 1990. Wetlands Losses in the United States, 1780s to 1980s. U.S. Department of the Interior, Fish and Wildlife Service, Washington, DC.

Dahl, T. W., C. E. Johnson, and W. E. Frayer. 1991. Wetland Status and Trend in the Conterminous United States, Mid-1970s to Mid-1980s. U.S. Department of the Interior, Fish and Wildlife Service, Washington, DC.

Daily, G. C. 1997. Nature's Services: Societal Dependence on Natural Ecosystems. Island Press, Washington, DC.

Damman, A. W. H., and T. W. French. 1987. The Ecology of Peat Bogs of the Glaciated Northeastern United States: A Community Profile. U.S. Fish and Wildlife Service Biological Report 85(7.16):100.

Danks, H. V. 1971. Overwintering of some north temperate and arctic Chironomidae. II Chironomid biology. Canadian Entomologist 103:1875–1910.

Davis, S. M., and J. C. Ogden (eds.). 1994. Everglades: The Ecosystem and Its Restoration. St. Lucie Press, Delray Beach, FL.

Davis, M. M., S. W. Sprecher, J. S. Wakely, and G. R. Best. 1996. Environmental gradients and identification of wetlands in north-central Florida. Wetlands 16:512–523.

de Szalay, F. A., D. P. Batzer, and F. H. Resh. 1996. Mesocosm and macrocosm experiments to examine effects of mowing emergent vegetation on wetland invertebrates. Environmental Entomology 25:203–209.

de Szalay, F. A., and V. H. Resh. 1997. Responses of wetland invertebrates and plants important in waterfowl diets to burning and mowing of emergent vegetation. Wetlands 17:149–156.

Delorme, L. D. 1991. Ostracoda. Pages 691–722 *in* J. H. Thorp and A. P. Covich (eds.), Ecology and Classification of North American Freshwater Invertebrates. Academic Press, New York.

Denno, R. F., and E. E. Grissell. 1979. The adaptiveness of wing-dimorphism in the salt-marsh inhabiting planthopper, *Prokelisia marginata* (Homoptera: Delphacidae). Ecology 6:221–236.

Denno, R. F., and G. K. Roderick. 1992. Density-related dispersal in planthoppers: Effects of interspecific crowding. Ecology 73:1323–1334.

Diehl, J. K., H. J. Holliday, C. J. Lindgren, and R. E. Roughly. 1997. Insects associated with purple loosestrife, *Lythrum salicaria,* in southern Manitoba. Canadian Entomologist 129:937–948.

Doak, D. F., and L. S. Mills. 1994. A useful role for theory in conservation. Ecology 75:15–626.

Dodson, S. I. 1970. Complementary feeding niches sustained by size-selective predation. Limnology and Oceanography 15:131–137.

———. 1974. Zooplankton competition and predation: An experimental test of the size-efficiency hypothesis. Ecology 55:605–613.

Dodson, S. I., and D. G. Frey 1991. Cladocera and other Branchiopoda. Pages 725–786 *in* J. H. Thorp and A. P. Covich (eds.), Ecology and Classification of North American Freshwater Invertebrates. Academic Press, New York.

Drake, J. A. 1991. Community-assembly mechanics and the structure of an experimental species ensemble. American Naturalist 137:1–26.

Eldridge, J. 1990. Aquatic invertebrates important for waterfowl production. Fish and Wildlife Leaflet 13.3.3. U.S. Fish and Wildlife Service, Washington, DC.

Environmental Laboratory. 1987. Corps of Engineers Wetlands Delineation Manual. Technical Report Y-87-1. U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS.

Epperson, J. E. 1992. Missouri Wetlands: A Vanishing Resource. Missouri Department of Natural Resources: Division of Geology and Land Survey. Water Resources Report No. 39.

Erwin, K. 1991. An Evaluation of Wetland Mitigation in the South Florida Water Management District. Volume I. Report to the South Florida Water Management District, West Palm Beach, FL.

Federal Interagency Committee for Wetland Delineation. 1989. Federal Manual for Identifying and Delineating jurisdictional wetlands. Cooperative Technical Publication, U.S. Army Corps of Engineers, U.S. Environmental Protection Agency, U.S. Fish and Wildlife Service, and U.S.D.A. Soil Conservation Service, Washington, DC.

Feminella, J. W., and V. H. Resh. 1989. Submersed macrophytes and grazing crayfish: An experimental study of herbivory in a California freshwater marsh. Holarctic Ecology 12:1–18.

Fernando, C. H. 1959. The colonization of small freshwater habitats by aquatic insects. 2. Hemiptera. Ceylon Journal of Science 2:5–32.

Fernando, C. H., and D. Galbraith. 1983. Seasonality and dynamics of aquatic insects colonizing small habitats. Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen 18:1564–1575.

Findlay, C. S., and J. Houlahan. 1997. Anthropogenic correlates of species richness in south-eastern Ontario wetlands. Conservation Biology 11:1000–1009.

Findlay, S., K. Howe, and H. K. Austin. 1990. Comparison of detritus dynamics in two tidal freshwater wetlands. Ecology 71:288–295.

Foster, A. P., and D. A. Procter. 1995. The occurrence of some scarce East Anglian fen invertebrates in relation to vegetation management. Pages 223–240 *in* B. D. Wheeler, S. C. Shaw, W. J. Fojt, and R. A. Robertson (eds.), Restoration of Temperate Wetlands. John Wiley & Sons, New York.

France, R. L. 1997. The importance of beaver lodges in structuring littoral communities in boreal headwater lakes. Canadian Journal of Zoology 75:1009–1013.

Fredrickson, L. H. 1991. Strategies for Water Level Manipulations in Moist-soil Systems. U.S. Fish and Wildlife Leaflet 12.4.6, Washington, D.C.

Fredrickson, L. H., and F. A. Reid. 1988. Invertebrate Response to Wetland Management. U.S. Fish and Wildlife Leaflet 13.2.1, Washington, DC.

Fretwell, J. D., J. S. Williams, and P. J. Redman (eds.). 1996. National Summary on Wetland Resources. Water-Supply Paper 2425, U.S. Geological Survey, Washington, DC.

Frisbee, M. P., and R. E. Lee. 1997. Inoculative freezing and the problem of winter survival for freshwater macroinvertebrates. Journal of the North American Benthological Society 16:636–650.

Fry, B. 1991. Stable isotope diagrams of freshwater food webs. Ecology 72:2293–2297.

Galatowitsch, S. M., and A. G. van der Valk 1996. The vegetation of restored and natural prairie wetlands. Ecological Applications 6:102–112.

Gates, F. C. 1926. Plant succession about Lake Douglas, Cheboygan County, Michigan. Botanical Gazette 82:170–182.

Gibbs, J. P. 1993. Importance of small wetlands for the persistence of local populations of wetland-associated animals. Wetlands 13:25–31.

Gilpin, M. E., and I. A. Hanski 1991. Metapopulation Dynamics: Empirical and Theoretical Investigations. Academic Press, London.

Gitay, H., J. B. Wilson, and W. G. Lee. 1996. Species redundancy: A redundant concept. Journal of Ecology 84:121–124.

Goldsborough, L. G., and G. C. Robinson.1996. Algal ecology: Patterns in wetlands. Pages 77–117 *in* R. J. Stevenson, M. L. Bothwell, R. L. Lowe (eds.), Algal Ecology: Freshwater Benthic Systems. Academic Press, New York.

Golladay, S. W., B. W. Taylor, and B. J. Palik. 1997. Invertebrate communities of forested limesink wetland in southwest Georgia, USA: Habitat use and influence of extended inundation. Wetlands 17:383–393.

Good, R. E., D. F. Whigham, and R. L. Simpson. 1978. Freshwater Wetlands: Ecological Processes and Management Potential. Academic Press, New York.

Government of Canada. 1991. Federal Policy on Wetland Conservation. Environment Canada, Ottawa, ON.

Gower, A. M. 1967. A study of *Limnephilus lunatus* (Trichoptera: Limnephilidae) with reference to its life cycle in watercress beds. Transactions of Royal Entomological Society London 119:283–302.

Goyer, R. A., G. J. Lenhard, and J. D. Smith. 1990. Insect herbivores of a bald-cypress/tupelo ecosystem. Forest Ecology and Management 33/34:517–521.

Grover, A. M., and G. A. Baldassarre. 1995. Bird species richness within beaver ponds in south-central New York. Wetlands 15:108–118.

Hairston, N. G., Jr. 1987. Diapause as a predator avoidance adaptation. Pages 281–290. *In* W. C. Kerfoot and A Sih (eds.), Predation: Direct and Indirect Impacts on Aquatic Communities. University Press of New England, Hanover, NH.

———. 1996. Phenotypic variation in a zooplankton egg bank. Ecology 77:2382–2393.

Hairston, N. G., Jr., T. A. Dillon, and B. T. DeStasio. 1990. A field test for the cues of diapause in a freshwater copepod. Ecology 71:2218–2223.

Hanski, I. A., and M. E. Gilpin 1997. Metapopulation Biology: Ecology, Genetics, and Evolution. Academic Press, New York.

Hanski, I., and D. Simberloff. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. Pages 5–26 *in* I. A. Hanski and

M. E. Gilpin (eds.), 1997. Metapopulation Biology: Ecology, Genetics, and Evolution. Academic Press, New York.

Hanson, M. A., and M. G. Butler. 1994. Responses to food web manipulation in a shallow waterfowl lake. Hydrobiologia 279/280:457–466.

Harrison, R. B. 1980. Dispersal polymorphisms in insects. Annual Review of Ecology Systematics 11:95–118.

Harrison, S., and L. Fahrig. 1995. Landscape pattern and population conservation. Pages 298–308 *in* L. Hansson, L. Fahrig, and G. Merriam (eds.), Mosaic Landscapes and Ecological Processes. Chapman & Hall, New York.

Haukos, D. A., and L. M. Smith. 1994. Composition of seed banks along an elevational gradient in playa wetlands. Wetlands 14:301–307.

Heck, K. L., and L. B. Crowder. 1991. Habitat structure and predator-prey interactions in vegetated systems. Pages 381–299 *in* S. S. Bell, E. D. McCoy, and H. R. Mushinsky (eds.), Habitat Structure: The Physical Arrangement of Objects in Space. Chapman & Hall, New York.

Jackson, M. E., and R. D. Semlitsch. 1993. Paedomorphosis in the salamander *Ambystoma talpoideum*: Effects of a fish predator. Ecology 74:342–350.

Jeffries, M. 1994. Invertebrate communities and turnover in wetland ponds affected by drought. Freshwater Biology 32:603–612.

Jeffries, M., and D. Mills. 1990. Freshwater Ecology: Principles and Applications. Belhaven Press, London, UK.

Jordan, F., C. J. DeLeon, and A. C. McCreary. 1996. Predation, habitat complexity, and distribution of the crayfish *Procambarus alleni* within a wetland habitat mosaic. Wetlands 16:452–457.

King, R. S., and D. A. Wrubeleski. 1998. Spatial and diel availability of flying insects as potential duckling food in prairie wetlands. Wetlands 18:100–114.

Kirkman, L. K., and R. R. Sharitz. 1994. Vegetation disturbance and maintenance of diversity in intermittently flooded Carolina bays in South Carolina. Ecological Applications 4:177–188.

Korner, C. 1993. Scaling from species to vegetation: The usefulness of functional groups. Pages 117–132 *in* E. D. Schulze and H. A. Mooney (eds.), Biodiveristy and Ecosystem Function. Springer-Verlag, New York.

Krapu, G. L., R. J. Greenwood, C. P. Dwyer, K. M. Draft, and L. M. Corwardin. 1997. Wetland use, settling in patterns, and recruitment in mallards. Journal of Wildlife Management 61:736–746.

Lamberti, G. A., and J. W. Moore. 1984. Aquatic insects as primary consumers. Pages 164–195 *in* V. H. Resh and D. M. Rosenberg (eds.), The Ecology of Aquatic Insects. Praeger, New York.

Kusler, J. A., and M. E. Kentual (eds.). 1990. Wetland Creation and Restoration: The Status of the Science. Island Press, Washington, DC.

Landin, J., and K. Vepsalainen. 1977. Spring dispersal flights of pond-skaters, *Gerris* sp. (Heteroptera). Oikos 29:156–160.

Lajtha, K., and R. H. Michener (eds.). 1996. Stable Isotopes in Ecology and Environmental Science (Methods in Ecology). Blackwell Scientific, Oxford, UK.

Lawler, S. P., and P. J. Morin. 1993. Food web architecture and population dynamics in laboratory microcosms of protists. American Naturalist 141:675–686.

Lee, R. E. 1989. Insect cold hardiness: To freeze or not to freeze? Bioscience 39:308–313.

Leslie, A. J., T. L. Crisman, J. P. Prenger, and K. C. Ewel. 1997. Benthic macroinvertebrates of small Florida pond cypress swamps and the influence of dry periods. Wetlands 17:447–455.

Lugo, A. E., M. M. Brinson, and S. L. Brown (eds.). 1990. Forested Wetlands, Ecosystems of the World 15. Elsevier, Amsterdam, The Netherlands.

MacArthur, R. H., and E. O. Wilson. 1964. The Theory of Island Biogeography. Princeton University Press, Princeton, NJ.

Magee, P. A. 1993. Detrital Accumulation and Processing in Wetlands. Fish and Wildlife Leaflet 12.3.14. U.S. Fish and Wildlife Service, Washington, DC.

Malecki, R. A., B. Blossey, S. D. Hight, D. Schroeder, and L. T. Kok. 1993. Biological control of purple loosestrife. Bioscience 43:680–686.

McCafferty, W. P. 1983. Aquatic Entomology: The Fisherman's and Ecologist's Illustrated Guide to Insects and Their Relatives. Jones & Bartlett, Boston.

McElligott, P. E. K., and D. J. Lewis. 1994. Relative efficiencies of wet and dry extraction techniques for sampling macroinvertebrates in a a subarctic peatland. Memoirs of the Entomological Society of Canada 169:285–289.

McGrady-Steed, J., P. M. Harris, and P. J. Morin. 1997. Biodiversity regulates ecosystem predictability. Nature 390:162–165.

McPeek, M. A. 1989. Differential dispersal tendencies among *Enallagma* damselflies (Odonata) inhabiting different habitats. Oikos 56:187–195.

———. 1990a. Determination of species composition in the *Enallagma* damselfly assemblages of permanent lakes. Ecology 71:83–98.

———. 1990b. Behavioral differences between *Enallagma* species (Odonata) influencing differential vulnerability to predators. Ecology 71:1714–1726.

———. 1996. Tradeoffs, food web structure, and the coexistence of habitat specialists and generalists. American Naturalist 148:S124–S138.

Menge, B. A., J. Lubchenco, S. D. Gaines, and L. R. Ashkenas. 1986. A test of the Menge-Sutherland model of community organization in a tropical rocky intertidal food web. Oecologia 71:75–89.

Merritt, R. W., and K. W. Cummins (eds.). 1996. An Introduction to the Aquatic Insects of North America (3rd ed.). Kendall/Hunt, Dubuque, IA.

Michiels, N. K., and A. A. Dhondt. 1991. Characteristics of dispersal in sexually mature dragonflies. Ecological Entomology 16:449–459.

Minshall, G. W. 1996. Organic matter budgets. Pages 591–605 *in* F. R. Hauer and G. A. Lamberti (eds.), Methods in Stream Ecology. Academic Press, New York.

Mitsch, W. J., and J. G. Gosselink. 1993. Wetlands (2nd ed.). Van Nostrand Reinhold, New York.

Mitsch, W. J., and R. F. Wilson. 1996. Improving the success of wetland creation and restoration with know-how, time, and self-design. Ecological Applications 6:77–83.

Moloney, K. A., and S. A. Levin. 1996. The effects of disturbance architecture on landscape-level population dynamics. Ecology 77:375–394.

Morin, P. J., and S. P. Lawyer. 1995. Food web architecture and population dynamics: Theory and empirical evidence. Annual Review Ecology and Systematics 26:505–529.

Myers, R. L., and J. J. Ewel (eds.). 1990. Ecosystems of Florida. University of Central Florida, Orlando, FL.

Naeem, S. 1998. Species redundancy and ecosystem reliability. Conservation Biology 12:39–45.

Naeem, S., and S. Li. 1997. Biodiversity enhances ecosystem reliability. Nature 390: 507–509.

Naeem, S., L. J. Thompson, S. P. Lawyer, J. H. Lawton, and R. M. Goodwin. 1994. Declining biodiversity can alter the performance of ecosystems. Nature 369:734–737.

Naeem, S., L. J. Thompson, S. P. Lawyer, J. H. Lawton, and R. M. Goodwin. 1995. Biodiversity and ecosystem functioning: Empirical evidence from experimental microcosms. Philosophical Transactions of the Royal Society, London B 347:249–262.

Naiman, R. J., and H. Decamps 1997. The ecology of interfaces: Riparian zones. Annual Review of Ecology and Systematics 28:621–658.

Nilsson, A. N. 1986. Life cycles and habitats of the northern European Agabini (Coleoptera: Dytiscidae). Entomologica Basiliensia 11:391–347.

Nordstrom, L. H., and M. R. Ryan. 1996. Invertebrate abundance at occupied and potential piping plover nesting beaches: Great Plains alkali wetlands vs. the Great Lakes. Wetlands 16:429–435.

Odum, W. E. 1988. Comparative ecology of tidal freshwater and salt marshes. Annual Review of Ecology and Systematics 19:147–176.

Olson, E. J., E. S. Engstrom, M. R. Doeringsfeld, and R. Bellig. 1995. Abundance and distribution of macroinvertebrates in relation to macrophyte communities in a prairie marsh, Swan Lake, Minnesota. Journal of Freshwater Ecology 10:325–335.

O'Neill, M. P., J. C. Schmidt, J. P. Drobrowolski, C. P. Hawkins, and C. M. U. Neale. 1997. Identifying sites for riparian wetland restoration: Application of a model to the upper Arkansas River Basin. Restoration Ecology 5:85–102.

Osenburg, C. W., and G. G. Mittlebach. 1996. The relative importance of resource limitations and predator limitation in food chains. Pages 134–148 *in* G. A. Polis and K. O. Winemiller (eds.), Food Webs: Integration of Patterns and Dynamics. Chapman & Hall, New York.

Oswood, M. W., L. K. Miller, and J. G. Irons. 1991. Overwintering of freshwater macro-invertebrates. Pages 360–375 *in* R. E. Lee and D. L. Denlinger (eds.), Insects at Low Temperature. Chapman & Hall, New York.

Otto, C. 1981. Why does duration of flight periods differ in caddisflies? Oikos 27: 383–386.

Paine, R. T. 1992. Foodweb analysis through field measurement of per capita interaction strength. Nature 355:73–75.

Pajunen, V. I., and J. Salmi. 1988. The winter habitats and spring dispersal of rockpool corixids (Heteroptera: Corixidae). Annales Entomologici Fennici 54:97–102.

Palmer, M. A., R. F. Ambrose, and N. L. Poff. 1997. Ecological theory and community restoration ecology. Restoration Ecology 5:291–300.

Pechman, J. H. K., D. E. Scott, J. W. Gibbons, and R. D. Semlitsch. 1989. Influence of wetland hydroperiod on diversity and abundance of metamorphosing juvenile amphibians. Wetlands Ecology and Management 1:3–11.

Peckarsky, B. L., P. R. Raissinet, M. A. Penton, and D. J. Conklin. 1990. Freshwater macroin-vertebrates of northeastern North America. Comstock Press, Ithaca, NY.

Peterson, B. J., and B. Fry. 1987. Stable isotopes in ecosystems studies. Annual Review of Ecology and Systematics. 18:293–320.

Playa Lakes Joint Venture. 1993. Accomplishment Report 1989–1992. North American Waterfowl Management Plan, U.S. Fish and Wildlife Service, Washington, DC.

Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: The Dynamics of Spatially Subsidized Food Webs. Annual Review of Ecology and Systematics 28:289–316.

Polis, G. A., and K. O. Winemiller (eds.). 1996. Food Webs: Integration of Patterns and Dynamics. Chapman & Hall, New York.

Pritchard, G. 1983. Biology of Tipulidae. Annual Review of Entomology 28:1–22.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652–661.

Pulliam, H. R., and B. J. Danielson. 1988. Sources, sinks, and habitat selection: A landscape perspective on population dynamics. American Naturalist 137:S50–S66.

Reice, S. R. 1994. Nonequilibrium determinants of ecological community structure. American Scientist 82:424–435.

Richardson, C. J., and E. J. McCarthy. 1994. Effects of land development and forest management on hydrologic response in southeastern wetlands: A review. Wetlands 14:56–71.

Richter, B. D., D. P. Braun, M. A. Mendelson, and L. L. Master. 1997. Threats to imperiled freshwater fauna. Conservation Biology 11:1081–1093.

Robinson, G. G. C., S. E. Gurney, and L. G. Goldsborough. 1997a. The primary production of benthic and planktonic algae in a prairie wetland under controlled water-level regimes. Wetlands 17:182–194.

———. 1997b. Response of benthic and planktonic algal biomass to experimental water-level manipulation in a prairie lakeshore wetland. Wetlands 17:167–181.

Rosenberg, D. M., and H. V. Danks. 1987. Aquatic insects of peatlands and marshes in Canada. Memoirs of Entomological Society of Canada.

Rowe, C. L., and W. A. Dunson. 1995. Impacts of hydroperiod on growth and survival of larval amphibians in temporary ponds of central Pennsylvania, USA. Oecologia 102:397–403.

Safran, R. J., C. R. Isola, M. A. Colwell, and O. E. Williams. 1997. Benthic invertebrates at foraging locations of nine waterbird species in managed wetlands of the northern San Joaquin Valley, California. Wetlands 17:407–415.

Schneider, D. W. 1997. Predation and food web structure along a habitat duration gradient. Oecologia 110:567–575.

Schneider, D. W., and T. M. Frost. 1996. Habitat duration and community structure in temporary ponds. Journal of the North American Benthological Society 15:64–86.

Semlitsch, R. D. 1987. Interactions between fish and salamander larvae. Oecologia 72: 482–486.

Sippel, W. S. 1988. Wetland Identification and Delineation Manual. Vol. I: Rationale, Wetland Parameters, and Overview of Jurisdictional Approach. April 1988 revised interim final. Office of Wetlands Protection, U.S. Environmental Protection Agency, Washington, DC.

Skelly, D. K. 1992. Field evidence for a behavioral antipredator response in a larval amphibian. Ecology 73:704–708.

———. 1995. A behavioral tradeoff and its consequences for the distribution of *Pseudacris* treefrog larvae. Ecology 76:150–164.

———. 1997. Tadpole communities. American Scientist 85:36–45.

Smith, R. D., A. Ammann, C. Bartoldus, and M. M. Brinson. 1994. An Approach for Assessing Wetland Functions Based on Hydrogeomorphic Classification, Reference Wetlands, and Functional Indices. Wetlands Research Program Technical Report WRP-DE-9. U.S. Army Engineers Waterways Experiment Station, Vicksburg, MS.

Soumille, H., and A. Thiery. 1997. A new quantitative sediment corer for sampling invertebrates across the mud water interface and soil of shallow rice fields. Annales de limnologie 33:197–203.

Southwood, T.R.E. 1977. Habitat, the templet for ecological strategies. Journal of Animal Ecology 46:337–365.

———. 1988. Tactics, strategies, and templets. Oikos 52:94–100.

Spence, J. R., and N. M. Anderson. 1994. Biology of water striders: Interactions between systematics and ecology. Annual Review of Entomology 39:101–128.

Sprules, W. G. 1972. Effects of size-selective predation and food competition on high altitude zooplankton communities. Ecology 53:375–386.

Stiehl, R. B. 1994. Habitat Evaluation Procedures (HEP) Workbook. National Biological Survey. National Ecological Resources Center, Fort Collins, CO.

Tauber, J. J., C. A. Tauber, and S. Masaki. 1986. Seasonal Adaptations of Insects. Oxford University Press, New York.

Thorp, J. H., and A. P. Covich (eds.). 1991. Ecology and Classification of North American Freshwater Invertebrates. Academic Press, New York.

Tilman, D., and J. A. Downing. 1994. Biodiversity and stability in grasslands. Nature 367:363–365.

Tilman, D., J. A. Downing, and D. A. Wedin. 1994. Does diversity beget stability? Nature 371:257–264.

Tilman, D., D. Wedin, and J. Knops. 1996. Biodiversity and sustainability influenced by biodiversity in grassland ecosystems. Nature 379:718–720.

Tiner, R. W. 1984. Wetlands of the United States: Current Status and Recent Trends. U.S. Fish and Wildlife Service, National Wetlands Inventory, Washington, DC.

———. 1989. Wetland boundary delineation. Pages 232–248 *in* R. P. Brooks, F. J. Brenner, and R. W. Tiners (eds.), Wetlands Ecology and Conservation: Emphasis in Pennsylvania. The Pennsylvania Academy of Science, Philadelphia, PA.

———. 1991. The concept of a hydrophyte for wetland identifications. BioScience 41: 236–247.

———. 1993a. Using plants as indicators of wetland. Proceedings of the Academy of Natural Sciences of Philadelphia 144:240–253.

———. 1993b. The primary indicators methods—a practical approach to wetland recognition and delineations in the United States. Wetlands 13:50–64.

———. 1996. Wetland definitions and classifications in the United States. Pages 27–34 *in* Water-Supply Paper 2425, J. D. Fretwell, J. S. Williams, and P. J. Redman (eds.), National Summary on Wetland Resources. U.S. Geological Survey, Washington, DC.

Turner, A. M., and J. P. McCarty. 1998. Resource availability, breeding site selection, and reproductive success of red-winged blackbirds. Oecologia 113:140–146.

Turner, A. M., and J. C. Trexler. 1997. Sampling aquatic invertebrates from marshes: Evaluating the options. Journal of the North American Benthological Society 16: 694–709.

Van der Valk, A. G. 1981. Succession in wetlands: A Gleasonian approach. Ecology 62:688–696.

Van der Valk, A. G., and C. B. Davis 1978. The role of seed banks in the vegetation dynamics of prairie glacial marshes. Ecology 59:322–325.

VanRees-Siewert, K. L., and J. L. Dinsmore 1996. Influence of wetland age on bird use of restored wetlands in Iowa. Wetlands 16:577–582.

Ward, J. V. 1992. Aquatic Insect Ecology. Vol. 1. Biology and Habitat. John Wiley & Sons, New York.

Webster, J. R., and E. F. Benfield. 1986. Vascular plant breakdown in freshwater ecosystems. Annual Review of Ecology and Systematics 17:567–594.

Welch, P. S. 1952. Limnology. McGraw-Hill, New York.

Wellborn, G. A. 1994. Size-biased predation and the evolution of prey life histories: A comparative study of freshwater amphipod populations. Ecology 75:2104–21017.

Wellborn, G. A., D. K. Skelly, and E. E. Werner. 1996. Mechanisms creating community structure across a freshwater habitat gradient. Annual Review of Ecology and Systematics 27:337–363.

Welling, C. H., R. L. Pederson, and A. G. Van der Valk. 1988. Recruitment from the seed bank and the development of zonation of emergent vegetation during a drawdown in a prairie wetland. Journal of Ecology 76:483–496.

Werner, E. E., and B. R. Anholt. 1993. Ecological consequences of the tradeoff between growth and mortality rates mediated by foraging activity. American Naturalist 142:242–272.

Werner, E. E., and M. A. McPeek 1994. Direct and indirect effects of predators on two anuran species along an environmental gradient. Ecology 75:1368–1382.

Wetzel. R. G. 1983. Limnology (2nd ed.), Saunders College, Philadelphia, PA.

Wharton, C. H., W. M. Kitchens, E. C. Pendleton, and T. W. Sipe. 1982. The Ecology of Bottom-land Hardwood Swamps of the Southeast: A Community Profile. U.S. Fish and Wildlife Service, Biological Services Program FWS/OBS-81/37.

Wheeler, B. D., S. C. Shaw, W. J. Fojt, and R. A. Robertson. 1995. Restoration of Temperate Wetlands. John Wiley & Sons, New York.

Wiggins, G. B. 1973. A contribution to the biology of caddisflies (Trichoptera) in temporary pools. Life Science Contributions of the Royal Ontario Museum 88:1–28.

———. 1996. Larvae of the North American caddisflies (Trichoptera) (2nd ed.). University of Toronto Press, Toronto, ON.

Wiggins, G. B., R. J. Mackay, and I. M. Smith. 1980. Evolutionary and ecological strategies of animals in annual temporary pools. Archive für Hydrobiologie Supplement 58:97–206.

Wilbur, H. M. 1997. Experimental ecology of food webs: Complex systems in temporary ponds. Ecology 78:2279–2302.

Williams, D. D. 1987. The Ecology of Temporary Waters. Timber Press, Portland, OR.

Williams, D. D., and B. W. Feltmate. 1992. Aquatic Insects. CAB International, Oxford, UK.

Williams, R. N., M. S. Ellis, and D. S. Fickle 1996. Insects in the Killbuck Marsh Wildlife Area, Ohio. 1994 Survey. Ohio Journal of Science 96:34–40.

Williamson, C. E. 1991. Copepoda. Pages 787–822 *in* J. H. Thorp and A. P. Covich (eds.), Ecology and Classification of North American Freshwater Invertebrates. Academic Press, New York.

Wilson, J. B., and R. J. Whittaker. 1995. Assembly rules demonstrated in a salt-marsh community. Journal of Ecology 83:801–807.

Wilson, R. F., and W. J. Mitsch. 1996. Functional assessment of five wetlands constructed to mitigate wetland loss in Ohio, USA. Wetlands 16:436–451.

Windell, J. T., B. E. Willard, D. J. Cooper, S. Q. Foster, C. F. Knud-Hansen, L. P. Rink, and G. N. Kiladis. 1986. An Ecological Characterization of Rocky Mountain Montane and Subalpine Wetlands. U.S. Fish and Wildlife Service Biology Report 86 (11).

Winemiller, K. O. 1996. Factors driving temporal and spatial variation in aquatic floodplain food webs. Pages 298–312 *in* G. A. Polis and K. O. Winemiller (eds.), Food Webs: Integration of Patterns and Dynamics. Chapman & Hall, New York.

Wissinger, S. A. 1997. Cyclic colonization and predictable disturbance: A template for biological control in ephemeral crop systems. Biological Control 10:4–15.

Wissinger, S. A., and H. H. Whiteman. 1992. Fluctuation in a Rocky Mountain population of salamanders: Anthropogenic acidification or natural variation? Journal of Herpetology 26:377–391.

Wissinger, S. A., and W. S. Brown. Habitat permanence, life histories and the distribution of five caddisfly species in subalpine wetlands in central Colorado (unpub. ms).

Wissinger, S. A., G. B. Sparks, G. L. Rouse, W. S. Brown, and H. Steltzer. 1996. Intraguild predation and cannibalism among larvae of detritivorous caddisflies in subalpine wetlands. Ecology 77:2421–2430.

Wissinger, S. A., H. H. Whiteman, G. B. Sparks, G. L. Rouse, and W. S. Brown. 1999. Tradeoffs between competitive superiority and vulnerability to predation in caddisflies along a permanence gradient in subalpine wetlands. Ecology. 80: In press.

Young, E. C. 1965. The incidence of flight polymorphism in British Corixidae and description of the morphs. Journal of Zoology 146:567–576.