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ECOLOGY OF INSECT COMMUNITIES IN NONTIDAL WETLANDS

Darold P. Batzer
Department of Biology, Canisius College, Buffalo, New York 14208

Scott A. Wissinger
Departments of Biology and Environmental Science, Allegheny College, Meadville, Pennsylvania 16335 and Rocky Mountain Biological Laboratory, Crested Butte, Colorado 81224

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ABSTRACT

Published research about wetland insects has proliferated, and a conceptual foundation about how wetland insect populations and communities are regulated is being built. Here we review and synthesize this new body of work. Our review begins with a summary of insect communities found in diverse wetland types, including temporary pools, seasonally flooded marshes, perennially flooded marshes, forested floodplains, and peatlands. Next, we critically discuss research on the population and community ecology of wetland insects, including the importance of colonization strategies and insect interactions with the physical environment, plants, predators, and competitors. Results from many of the experimental studies that we review indicate that some commonly held beliefs about wetland insect ecology require significant reevaluation. We then discuss the importance of wetland insect ecology for some applied concerns such as efforts to manage wetland insect resources as waterfowl food and development of ecologically sound strategies to control pest mosquitoes. We conclude with a discussion of wetland conservation, emphasizing insect aspects.

PERSPECTIVES AND OVERVIEW

The amount of published research on wetland insect communities has grown steadily since the mid 1980s. One reason for this increase is that insect communities in small wetlands have proven to be useful systems for testing

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Annual Reviews
www.annualreviews.org/aronline

ecological paradigms. Both community structure of insects and the environment of small wetlands can be readily manipulated or mimicked for experimental investigation (e.g. 11, 81, 115, 180, 184, 195). The newfound interest in the community ecology of wetland insects also is evident in the applied sector. Endangered wetland ecosystems are receiving a great deal of public attention, and the importance of insects in these systems is being recognized. In addition, waterfowl and pest management concerns about wetlands now place a high priority on information about insect ecology. In the 1960s and 1970s, wildlife workers discovered that insects were important waterfowl foods (120), and much of the recent research on wetland insects has been sponsored by wildlife interests. In addition, although mosquitoes have always been a research focus in wetlands, investigators currently take an increasingly holistic approach and study wetlands in a community context. Much of our understanding about how wetland insect communities are regulated comes from this applied work.

Although research on wetland insects has proliferated worldwide, recent reviews have focused on particular regions and specific wetland types (55, 90, 119, 154). Reviews of Canadian wetlands have been some of the most thorough (55, 154). Reviews of individual insect groups provide additional sources of information about wetland insects (33, 72, 99, 141, 171). Much of the early work on wetland insects is covered by Wiggins et al (189).

The theoretical foundations of insect population and community regulation in wetlands remain in the initial stages of development. One finds little mention of the important insect fauna in general reviews of wetland ecology (e.g. 22, 113) or in standardized field procedures to evaluate the biotic integrity of wetland habitats (3, 174). Researchers of wetland insects have typically used ecological models developed in other habitats as the basis for their work (e.g. 103, 119), and only recently have they begun to experimentally test and develop paradigms that specifically apply to wetlands. Those efforts are the major focus of our review, and we contend that many commonly held beliefs about wetland insect ecology require significant reevaluation.

We begin by reviewing the characteristics of insect communities found in diverse wetland types. We restrict our coverage to temporary pools, nontidal marshes, forested floodplains, and peatlands. Large wetlands, such as the Florida Everglades, include several of these wetland categories (143). We do not address tidal marshes because of space limitations. We then discuss the population and community ecology of wetland insects, including patterns of colonization and insect interactions with the physical environment, plants, predators, and competitors. We develop these themes using work conducted specifically in wetlands and refrain from forcing ecological paradigms developed in other habitats on wetland insect communities. We conclude with a discussion of applied aspects of wetland insect ecology such as insects and

Annual Reviews
www.annualreviews.org/aronline

waterfowl management, pest-insect control, and insect aspects of wetland conservation.

WETLAND INSECT COMMUNITIES

Temporary Pools

The smallest and often the most ephemeral of the wetlands are temporary pools that fill from seasonal rains or snow melt (131, 189, 190). Some flood and dry repeatedly (131); others fill for a few months (92, 131, 189); and some remain flooded for much of the year (131, 189). Most of the research on temporary-pool insects focuses on their adaptations for and interactions with the short-term flooding regimes. Another major area of research addresses biotic interactions.

Insects use various life-history strategies to survive in temporary pools. Many have methods for resisting drought (83, 189, 190), whereas others combine rapid aerial colonization and larval development to effectively avoid drought (189, 190, 194). However, drought is often a major mortality factor for insects in temporary pools (81, 150). Many species are habitat generalists that also flourish in more permanent wetlands (70, 124).

Temporary pools have especially diverse beetle and midge communities (4, 70, 92, 129, 160, 189). Among the different wetland types, temporary pools are unique in that mosquito larvae are often the numerically dominant residents (117, 150). Specific community structures are strongly influenced by the flooding regimes of individual pools (44, 131, 189) (see section on hydrology, below). In addition to wet-dry cycles, other abiotic factors that commonly affect insects include pool size (8, 130, 156) and water temperature (8, 130). Insect productivity can be very high in temporary pools (124, 189), possibly because decomposition during waterless stages enhances detrital food quality (189).

Biotic interactions often regulate wetland insect populations in temporary pools. This observation is somewhat surprising given the relatively short periods available for insects to interact with each other. High densities can lead to competitive interactions (82, 115, 150, 180). In these fishless habitats, predaceous insects can become very abundant (92), and they are often the top aquatic predators (see section on predation).

Seasonally Flooded Marshes

Seasonally flooded meadows or marshes are also highly ephemeral wetlands. Extensive stands of moist-soil annual plants and hydrophilic perennials are a unique feature of these habitats (147). Seasonally flooded marshes were historically common on river floodplains, but most have disappeared because of

Annual Reviews
www.annualreviews.org/aronline

river regulation (1, 147). This type of natural habitat still occurs over large portions of the Florida Everglades (143). Because seasonally flooded marshes are productive habitats for ducks, similar types of habitats are often constructed (e.g. moist-soil management units) and maintained artificially on waterfowl management areas (147). These managed habitats are where most insect research in seasonally flooded marshes has been done, and much of this research focuses on the impact of human manipulations on insect communities (12, 49, 52, 101, 147).

In managed seasonally flooded marshes, insects typically dominate the macroinvertebrate communities (12, 49, 52, 101, 125). Perhaps because of the intensive management, opportunists flourish. For example, rat-tailed maggots were very abundant in a managed California habitat (12), but reference to their occurrence elsewhere is scant. Typically, a few insect families dominate the communities of managed seasonal marshes, with the midges being particularly prominent (12, 49, 52, 125, 152). A beneficial aspect of such dominance in terms of waterfowl management is that midges in the genus *Chironomus* thrive in managed habitats (10, 12, 49, 52, 102), and they are often preferred duck food (10, 52, 102). Predatory insects are often very abundant (10, 12, 13, 49, 101, 125, 152), and like in temporary pools, they can become important community regulators (e.g. 11).

Perennially Flooded Marshes

Extensive stands of emergent aquatic plants are distinctive features of perennial-water marshes, and submersed macrophytes and algae are also conspicuous. As a result, much of the research on marsh insects involves their interactions with plants. Emergents are particularly important resources for marsh insects. Terrestrial or semiaquatic forms feed on above-water portions of emergent plants (27, 56) or use that area as habitat (51). Decaying plant material provides food for aquatic detritivores (28, 126). Submersed portions of living and dead emergent plants serve as habitat for numerous aquatic insects (9, 28, 51, 121). The habitat templates created by interspersions of emergent plants and open water are particularly productive areas for insects (107, 127).

Submersed or floating weed beds also support many insects (15, 39, 106, 159, 198). Numerous collembolans, aphids, and water striders can be found at the air-water interface of weed beds (15). Many aquatic insects use submersed plant surfaces as habitat (15, 39, 136, 137, 159). Midge larvae can be particularly numerous on these surfaces, even more so than on emergent plants (15, 198). An important role of macrophytes to marsh insects may be in providing substrates for growth of periphytic algal foods (28, 68). Algae is another important food for many marsh insects (28, 59, 68, 126), and it is also used by midge larvae to construct tube cases (11).

Annual Reviews
www.annualreviews.org/aronline

Not all marsh insects intimately associate with plants. Mud substrates are productive areas of many marshes, particularly for benthic dipteran larvae (9, 101, 122). Benthos and certain nektonic insects can be more abundant in open water than emergent vegetation zones (9, 14, 90, 159). Deep, artificially created channels can support numerous marsh insects (23, 143). Some species migrate between open and emergent areas (35, 118), although the transitional zone itself is seldom a preferred habitat (118, 159).

Forested Floodplains

Forested wetlands or swamps typically occur on river or stream floodplains. In addition to the flooded woodlands, these habitats contain temporary pools, semipermanent backwater ponds, and shallow lakes (1, 62, 165). Depending on rainfall and elevation, floodplain habitats can be flooded year-round or for only short durations (38, 61, 165), and specific patterns of inundation influence invertebrate communities (165). Invertebrate productivities can be very high in such habitats (165), perhaps because aqueous nutrients from flowing channels (62) and leaf fall from trees (38, 105) enrich forested floodplains. The secondary productivity from adjacent wetlands probably has important implications for riverine habitat ecologies, given that the floodplains cover a larger surface area than the associated channels (61).

In terms of faunal diversity, insects, especially midges, can dominate the invertebrate communities of forested floodplains (61, 62, 102). Midges are the only insects that consistently reach high densities in such habitats (78, 100, 101, 105, 165). A few predatory insects can be important in terms of biomass and productivity (38, 61, 105, 165), but noninsects such as aquatic worms, mollusks, and crustaceans tend to dominate (38, 49, 61, 78, 100, 165). Unexpectedly, insect shredders adapted to consume tree leaves are often rare (38, 105).

Floodplains often share insect taxa with their associated channels (38, 61). Those taxa tolerant of low levels of dissolved oxygen prosper most in the wetland portion of these systems (38, 165). Lotic insects use floodplain wetlands to exploit the rich food resources and warmer water (1), to reproduce (1, 38), or to find a haven from predation (168). Predatory fish themselves move into floodplains to feed on aquatic invertebrates and trapped terrestrials (148). Many different terrestrial insects live on dry floodplains (65) or in tree foliage (64).

Forested floodplains are a prevalent wetland type in the southern latitudes, yet their invertebrate communities are understudied relative to other wetlands (49, 78, 114, 158, 165). Most research focuses on insects closely associated with channels, so even less is known about the fauna of difficult-to-access backswamps (165). Learning more about the ecology of invertebrate communities in these wetlands should become a research priority.

Annual Reviews
www.annualreviews.org/aronline

Peatlands

Peat develops in wetlands where decomposition does not keep pace with plant production (181). Peatlands are categorized as fens or bogs based on hydrology, with fens usually being dominated by sedges or other monocots and bogs by *Sphagnum* mosses (181). Peat accumulation causes peatland surfaces to gradually rise above the water table (181), and thus many of the insects found in these habitats are of terrestrial origin. Aquatic species can occur in the water around peatland vegetation itself (e.g. 155), although most of the research addressing the aquatic fauna has been conducted in peatland pools.

Finnamore & Marshall (55) recently edited an extensive review of the terrestrial arthropod fauna of Canadian peatlands; therefore, we emphasize research conducted elsewhere. Some of the terrestrial insects of peatlands are invaders from surrounding upland habitats (86). However, others are unique to peatlands (36, 98), and particular assemblages of terrestrial species can be useful in characterizing peatland habitats (36, 74). Ants are especially important ecologically because mound-building and hummock-dwelling species can influence vegetation patterns and habitat microtopography (30, 98).

A 1987 review by Rosenberg & Danks covers the truly aquatic insects of Canadian peatlands (154); this treatment also addressed research outside of Canada. The more recently published work indicates that, similar to the terrestrial fauna, the aquatic insect communities of peatlands consist of a mixture of invaders from other habitats and species unique to peatlands (155). Insects occur in diverse aquatic microhabitats, including saturated peat itself (138, 155), shallow pools (79, 138), and deeper ponds (25, 94). A unique habitat for some aquatic insects is the water that accumulates inside pitcher plants (54 and references therein). The deeper ponds of peatlands can be particularly productive habitats for insects (138). The relative size of pools (94), water temperature (25, 173), dissolved oxygen level (25), and water stability (79, 94) have all been identified as important abiotic regulators of aquatic peatland insects. Although many peatland pools are acidic, the primary influence of acid on insects is probably indirect. The lack of fish in acidic habitats may be a more important influence on insects than the water chemistry itself (73).

POPULATION AND COMMUNITY ECOLOGY

Colonization and Life-History Strategies

Many wetlands dry, either seasonally or unpredictably, during droughts, and invertebrates that thrive in these habitats exhibit two general strategies for rapid colonization during and after inundation. The first is desiccation resistance, which is best documented in flightless invertebrates (protists, rotifers, crustaceans, annelids, mollusks) that deposit resistant eggs or spores in the

Annual Reviews
www.annualreviews.org/aronline

substrate (189, 190). Many wetland insects, including dragonflies, caddisflies, beetles, and various dipterans, also have desiccation-resistant eggs (189). Many dipteran eggs are similar to the resistant stages of flightless invertebrates in that they are often deposited just before basins dry and, in their diapausal state, can resist harsh conditions (189, 190). In some mosquitoes and a few midges, egg maturation within clutches is staggered, thus providing an egg bank that remains viable over several dry-wet cycles (2, 190). Several wetland-inhabiting damselflies in wetlands deposit eggs endophytically in the stems of emergent plants, where the eggs undergo diapause until habitats reflood (48 and references therein). Insects that oviposit in dried wetlands typically enclose eggs in a protective gelatinous mass. Dry-basin oviposition has been especially well studied for several species of *Sympetrum* dragonflies from northern wetlands (177) and for limnephilid caddisflies that oviposit under rocks or wood in or near dry basins (16; SA Wissinger & WW Brown, unpublished data).

Desiccation resistance in adult aquatic insects is best documented for beetles that survive drying by burying themselves in the mud or crawling under rocks or logs in or near wetland basins (81, 92, 101, 189). Some odonate nymphs also resist drying and/or freezing by burying themselves in the substrate of dry habitats (33, 83). Desiccation resistance during the larval stage has been documented for most families of aquatic Diptera (101, 141, 189). Of these, the midges are often most abundant and widespread in moist soils under dried wetland basins (79, 189). Given that both the egg and larvae of midges can be desiccation resistant and adults are such good dispersers (see below), it is perhaps not surprising that they are often the most diverse and abundant insects in ephemeral habitats (26, 44, 61, 189, 190).

A second strategy that aquatic insects use to colonize wetlands involves adult immigration and oviposition. The most rapid aerial colonizers are opportunists such as mosquitoes and midges, which often deposit eggs within a few days after inundation (43, 89, 101, 150, 153, 183, 191). In several wetland insects, adult longevity facilitates colonization. For example, in limnephilid caddisflies, adults emerge just before ponds dry and diapause for a month or more in terrestrial habitats before returning to lay eggs (16, 99; SA Wissinger & WW Brown, unpublished data). Similarly, long-lived dragonfly adults survive the dry phase of wetland hydroperiods in the terrestrial environment and deposit eggs when basins refill (32, 94). Dragonfly colonization of newly inundated habitats is also aided by the general tendency to disperse beyond the limits of their natal habitats (111).

The most common strategy for the aerial colonization of ephemeral wetlands appears to involve cycles of migration between permanent and temporary aquatic habitats (189, 194). For example, in a seasonally flooded marsh that was managed as waterfowl habitat, all of the numerically dominant insects (various dipterans, a beetle, and a water boatman) colonized by immigrating

Annual Reviews
www.annualreviews.org/aronline

from nearby aquatic habitats rather than by means of desiccation-resistant stages (12). Our review of the literature suggests that this general pattern of "cyclic colonization" (sensu 194) is important for the maintenance of insect populations in many natural and managed wetlands, including seasonally and perennially flooded marshes (9, 12, 29, 70, 76, 122, 125, 128, 143, 144), temporary pools in larger wetland complexes (81, 94, 129), and tropical and temperate swamps (61, 101, 114, 158).

Cyclic colonization is best documented for adult hemipterans and beetles, which exhibit a characteristic life-history syndrome that often involves flight polymorphism (cf 72, 93, 171, 176). For beetles and hemipterans that inhabit temporary waters, long-lived adults typically overwinter in permanent habitats and then fly to newly inundated habitats in spring. Upon arrival, wing musculature histolyzes in the females, and the developing ovaries expand into the vacated space. Depending on the duration of the wet phase, one or more short-winged or wingless generations are completed, and then, as habitats dry, long-winged individuals with immature gonads emigrate and return to permanent refugia. Flight polymorphisms facilitate dispersal to and from permanent refugia and allows for the rapid establishment of large populations in the ephemeral habitat (72, 171). The importance of cyclic colonization for the maintenance of beetle populations in temporary habitats is emphasized by Svensson (176), who suggests that their absence in those habitats near the edges of geographical ranges is related to the relatively low density of source populations.

Although most cyclic colonization occurs between local habitats, several large dragonflies colonize ephemeral wetlands by migrating over long distances (34). In the tropics, these strong flyers complete several generations per year by tracking shifting monsoonal rains and exploiting temporary habitats across a latitudinal gradient (32). In North America, these dragonflies migrate to temperate wetlands and other fishless habitats where they complete one summer generation before emigrating south in autumn (193).

Influence of Physicochemical Variables

Wetland insects can be affected by several abiotic factors (e.g. 66), but only the influences of hydrology, acidity, or nutrient levels have been studied in detail. The periodic flooding and drying of wetland habitats is probably the most important single influence on insect communities, and the way wetland insects deal with drought is a key to their success (189). The research interest in acidity stems from concerns about acid pollution and curiosity about what impact low natural pH has on insects. Phosphorous and nitrogen levels are also a concern in terms of pollutants leading to eutrophication; conversely, research has examined how the natural nutrient-poor status of some wetlands

Annual Reviews
www.annualreviews.org/aronline

influences insects (28, 59, 123). Other physicochemical variables that can influence wetland insect communities are habitat sizes (8, 94, 156), high or low water temperatures (8, 25, 143, 173), and dissolved oxygen levels (25, 143, 144).

HYDROLOGY Water-level stability of wetlands is a major influence on insect community structure and productivity (9, 61, 81, 94, 131, 189). Highly ephemeral habitats tend to be dominated by beetles and mosquitoes, while midges and odonates predominate in habitats that are flooded longer (12, 70, 81, 94, 131, 159). Insects dependent on a drought-resistant stage are virtually eliminated when ephemeral habitats remain flooded (125). If wetlands are flooded infrequently or for short durations, their invertebrate productivities may be low (61). A long and intense drought phase can also have a negative impact on wetland invertebrates (44, 81).

Field observations indicate that invertebrates in temporary pools grow more rapidly than those in perennial water wetlands (142, 189). However, in the few reports that directly compare insects from each of these habitats, the efficiency of growth and feeding is actually higher for insects from perennial habitats. For example, Pritchard & Berté (142) found that a caddisfly adapted for perennially flooded habitats grew more efficiently than a species adapted for life in ephemeral pools, and they believed the more rapid growth of the latter species in the field was simply related to differences in habitat temperature. In addition, when populations of the same midge species living in temporary and perennial pools were compared, their feeding rates, feeding efficiencies, and productivities were all higher in the perennial habitat (124). The general belief that temporary pools are intrinsically more productive habitats for insects than perennially flooded habitats needs further evaluation.

ACIDITY Although some insects select wetland habitats with specific acidities (4, 66), experimental acidification of wetland habitats often has shown little impact on insects. For example, damselfly nymphs were not affected by pH regulation unless levels became very low (63). Experimental reduction of the pH of a fen peatland had no detectable influence on midge emergence (155). In contrast, low pH may actually benefit insects in some cases because insectivorous fish cannot survive in many acidic habitats (17, 73, 77, 139). However, low pH may harm certain insects. In studies contrasting acid and circumneutral wetlands, the acidic habitats supported fewer mayfly nymphs (17) or had detrital food resources of lower quality (89).

NUTRIENTS Descriptive studies indicate that nutrient levels may influence wetland insect communities (62, 66, 74, 107). However, excessive nutrient loading in the Florida Everglades increased invertebrate diversity (144), con-

Annual Reviews
www.annualreviews.org/aronline

trary to expectation (62, 66). A series of experiments in a nutrient-poor Canadian marsh found that naturally low phosphorous and nitrogen levels can limit midge productivity (28, 59, 123).

Primary Consumers

Many terrestrial insects in wetlands consume the foliage of living macrophytes (27, 56, 64, 103, 162). However, aquatic forms rarely eat living vascular plants (119, 167); instead they consume detritus from dead plants. Decomposing leaves and stems from wetland macrophytes (28, 119) and trees (38, 105) are important sources of detritus, as are inputs from riparian habitats and upland run-off (124, 133, 160). Algae are another food important to some wetland insects, particularly midge larvae (11, 28, 59, 68, 119).

Which of the above sources of plant carbon are most important to the aquatic food webs in wetlands is under debate (119). Recent studies that use molecular techniques (stable isotope analysis) indicate that aquatic insect and other invertebrate consumers commonly eat algal periphyton or emergent macrophytes (in the form of detritus) but rarely eat filamentous algae or detritus from submersed macrophytes (24, 112, 126). A surprising result of these studies was that unknown sources of carbon, rather than the conspicuous forms tested above, were important to some consumers (24, 126).

MACROPHYTE CONSUMERS Most wetland insects that consume living macrophytes occur on the above-water portions of the plants or bore inside them, and they tend to be members of primarily terrestrial groups (aphids, leaf beetles, weevils, moth caterpillars) (15, 56, 103, 162). Some of these herbivores can have a great impact on plant growth and survival (64, 103). Foote et al (56) list several published accounts of insect herbivores removing from 25 to 56% of the standing crop of wetland macrophytes. Certain moth larvae can completely defoliate swamp trees (64). A beetle that consumed only 6% of the available biomass of water lily leaves still had a marked impact on detrital inputs into a wetland (162). Thus, although the subject is largely unstudied, the impact of terrestrial insect herbivores on overall wetland ecosystem function is probably very significant.

DETRITUS CONSUMERS As aquatic macrophytes or tree leaves decompose, aquatic invertebrate numbers on this material tend to increase (28, 41, 89, 101, 128, 153, 167). This pattern may be related to the increasing palatability and protein content of the decaying plant material (166, 167), as indicated by experimental evidence from some wetlands. A comparison of natural and artificial litter showed that both types initially supported similar numbers of midges, but as the natural litter decayed, it became the preferred substrate (28).

Annual Reviews
www.annualreviews.org/aronline

However, field experimentation often fails to link wetland invertebrate abundance with detritus quality. Invertebrate colonization rates can be similar on plant litters of differing nutritional qualities (89, 128), and fewer invertebrates occurred on litter from fast-decaying *Equisetum fluviatile* than slower decaying *Carex rostrata* (41). In some cases, temporal changes in invertebrate numbers on decaying litter may simply reflect their life-history patterns (128) or natural colonization cycles (153).

An issue separate from detritus quality is its quantity. Our survey of the literature uncovered little experimental evidence that the available supply of detrital food in wetlands can be limiting to detritivores. Where wetland macrophytes were cut and the detritus removed, detritivore populations either were unaffected or showed unexpected increases (122, 125). In another experiment, albeit nonreplicated, detritus was added to a marsh enclosure, but the expected increase in detritivore numbers failed to materialize (5). In a detailed descriptive study, a midge that dominated the benthos of two different wetland pools consumed only 4.6–13.0% of the available detritus over the course of a year (124). In certain cases, the low oxygen conditions created by decomposing plant matter may reduce rather than increase invertebrate numbers, at least temporarily (59). However, some detritivorous mosquitoes can reach high enough densities in temporary pools that they compete for space, which leads to food shortages despite the presence of abundant supplies of detritus (150).

In some cases, however, the availability of plant litter and detritus resources may limit insect populations. As mentioned previously, the substitution of a nonnutritive substrate for plant litter can reduce midge numbers (28). Increases in plant litter biomass caused by above-normal flooding of a marsh resulted in more midges and other consumers, although whether the detritus served as food or habitat was unclear (121). Finally, in a small pond study, midge growth rates, but not densities, increased as a result of enriched microdetrital food supplies (145).

In some wetland habitats, invertebrate detritivores play an important role in litter decomposition (89). However, in many wetlands, shredders adapted to process plant litter are rare (38, 105). If invertebrate consumers are excluded from decaying plant litter, decomposition rates can remain unchanged (153). In wetlands, most plant decomposition is probably accomplished by leaching and through microbial pathways rather than via invertebrate processing (41, 89, 105, 153, 189).

ALGAL CONSUMERS In contrast to detritus, a relatively strong case can be made that algal food supplies may become limiting in wetland food webs. Experiments in a seasonally flooded marsh (11), a perennially flooded marsh (68), and simulated temporary pools (115) indicate that midge larvae can overgraze their algal food supplies, which may lead to intra- or interspecific

Annual Reviews
www.annualreviews.org/aronline

competition for food. Enrichment of marshes with nitrogen and phosphorous, either from experimental introductions or pollutants (28, 59, 144), can increase the algal food supply and with it numbers of invertebrate consumers (except see 123). Herbicide-induced reductions in algal biomass can limit numbers of insect consumers (45). The importance of algae to wetland food webs has probably been underestimated (119).

Wetland Plants as Habitat

Apart from providing food for insects, wetland plants also serve as structural habitat. Distributions of some nonherbivorous species have been predicted accurately from information about which plants dominate wetland habitats (e.g. 149). In marshes, some of the most productive areas for insects are where open water is interspersed with emergent and submersed plants (107, 127, 143). Experimentally creating such interspersions can increase numbers of many insect taxa (12, 87, 122). However, some taxa such as epiphytic fly larvae and free-swimming mosquito larvae prefer denser plant stands (12, 137). Although living emergent plants rarely support high densities of insects directly on their surfaces (50, 198), the litter that accumulates from them is valuable habitat for epiphytic and mining midges that live on or in this material (121). The substrates lying beneath emergent plant litter can also support high densities of benthic insects (50).

In contrast to emergent plants, submersed plants support large numbers of epiphytic insects on their surfaces (50, 198). However, aquatic insect or other invertebrate use of submersed plant habitats varies among plant species, and it has generally been assumed that differences in plant morphology and architecture are responsible (i.e. plants with more colonizable substrate would support the most invertebrates) (39, 50, 71, 80, 198). If all factors other than plant morphology are held constant, this hypothesis appears to be valid (80). However, in natural plant beds, the mechanisms controlling wetland invertebrate numbers are considerably more complex. Plants with the most finely dissected leaves do not necessarily support the most invertebrates (39). Submersed plants with similar morphologies but different growth cycles harbor different invertebrate communities (71), and communities also change as individual plant beds grow and senesce (15). In addition to the insects that occur directly on submersed plant surfaces, free-swimming insects find these plant beds to be valuable refuges from predators (14, 137).

Predator-Prey Interactions and Food Webs

Fish are typically abundant only in those wetlands that remain flooded over long periods of time and are deep enough to prevent winterkill. They also occur as transients that move in and out of lacustrine marshes and floodplains

Annual Reviews
www.annualreviews.org/aronline

with flood waters (61, 148). Numerous studies suggest that wetlands with fish will have lower insect diversity and lower biomass than those that are fishless (46, 76, 77, 104). Many of the taxa that fish prey upon most heavily are also important in the diets of migratory waterfowl (10). Thus, fish are usually considered unwanted predators by managers of waterfowl habitat (12, 52, 77, 104).

The insect communities in fish and fishless wetlands also differ because of the size-selective nature of fish predation. In wetlands without fish, large-bodied active predators such as odonate nymphs, beetle larvae, and hemipterans replace fish as the top aquatic predators in the food web (14, 20, 101, 180). The few species of large predatory insects that can coexist with fish exhibit various antipredator morphologies and behaviors that are not observed in congeneric species that thrive in fishless habitats (14, 20, 73, 84, 109). Fishless habitats that are perennially flooded tend to support the highest diversity and overall abundance of these large predators (49, 61, 94, 159, 171, 176, 192). The lack of an increase in detritivore numbers following enhanced detritus levels in fishless wetlands suggests that large invertebrate predators can control prey abundance (5, 145, 146).

All of the top insect predators in fishless habitats are generalists that will prey on nearly all other invertebrates, including each other (11, 20, 84, 129, 171, 195). When species share common prey and also eat each other [i.e. intraguild predation (see 140)], food web connections will be complex. For example, nymphs of the large dragonfly *Tramea lacerata* prey on smaller dragonflies and on various other taxa such as damselfly nymphs that are also eaten by the smaller dragonflies. The addition of *Tramea* to a community will have a direct negative impact on damselfly nymphs but also an indirect positive effect through reduced numbers of other dragonfly predators. The net impact of *Tramea* predation in a community context is much lower than would be predicted from experiments involving only *Tramea* and damselflies (195). In wetlands with many predatory insects, the community-level impacts of removing or adding a predator will be difficult to understand in the absence of manipulative experimentation.

Most large predatory insects in fishless habitats are also notoriously cannibalistic (6, 84, 130, 140, 171, 175, 180), which may play an important role in regulating their populations (180). A generalized diet, and specifically cannibalism, may be important for colonizing predators that arrive in temporary habitats before preferred prey are abundant (194). Cannibalism in ephemeral wetlands may ensure that at least some individuals complete development before habitats dry (196).

Many of the predatory insects consume zooplankton (84, 197). Because of the high surface area-to-volume ratio, linkages between the benthic and zooplankton communities in shallow lentic habitats like wetlands presumably

Annual Reviews
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should be stronger than those in lakes. Although Richardson et al (151) found little evidence for this hypothesis, more data from different wetland types are needed to determine if benthic and planktonic communities are tightly coupled.

Various adult and larval amphibians can be seasonally abundant in fishless marshes and forested wetlands. The eggs and/or larvae of these amphibians are eaten by predatory insects that thrive in ephemeral wetlands (19, 60, 88, 110, 157, 178, 179). Conversely, the tadpoles of many salamanders and a few frogs and toads are predatory and, in some habitats, can regulate the abundance of insects and influence the size distribution of their communities (18, 75, 188). Interactions among fish, amphibians, and predatory insects can be complex. For example, Werner & McPeek (187) found that bullfrog tadpoles, which coexist with fish in permanent habitats, are quite vulnerable to predation by dragonfly nymphs and salamander larvae, both of which are excluded by fish from permanent habitats (187). In contrast, green frog tadpoles, which are most abundant in ephemeral habitats, are more vulnerable to fish than to dragonfly or salamander predation (187). Clearly, hydroperiod will have an important impact on the assemblage of top aquatic predators in wetland communities.

Although wetlands are often described as being situated at the ecotone between aquatic and terrestrial ecosystems, surprisingly little information is available about the movement of energy across that ecotone. Much of the evidence about this phenomenon addresses bird consumption of wetland insects. Many dabbling ducks readily prey on wetland insects (120) (see section on insects and waterfowl management, below). Several other groups of birds, such as swallows, martins, and blackbirds, also rely heavily on wetland insects as prey, especially during the breeding season (17, 120, 135). Orians (134) concluded that the emergence of particularly important prey items such as damselflies can play an important role in the timing of reproduction in marsh-nesting blackbirds. During the breeding season, the impact of these birds on insect mortality can be extremely high. For example, while feeding nestlings, red-wing blackbirds captured 50% of all emerging dragonflies as they transformed on stems of emergent plants (192).

The degree to which aquatic insect communities are regulated by top-down (by predatory insects, fish, amphibians, or birds) or bottom-up processes (abundance of detritus and/or algae) has not been investigated for most wetlands. Several recent experimental studies, however, suggest that the relative importance of top-down and bottom-up control varies between and even within wetlands (11, 69, 125). In a seasonally flooded marsh, Batzer & Resh (11) manipulated vegetation density and found that the densities of beetle larvae (the top predator) were considerably lower in 100% than in

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50% vegetation plots. Beetle predation in the 100% vegetation plots was not sufficient to regulate midge populations, which were eventually limited by periphyton abundance (bottom-up control). In adjacent plots with 50% plant cover, the large numbers of beetle larvae were sufficient to control midge densities (top-down control), and in the absence of midges, periphyton abundance increased. Later when beetles emerged, midge populations in 50% plots rebounded in the presence of abundant periphyton. These results emphasize that regulation in wetland food webs can vary temporally depending on insect life-cycle dynamics and spatially depending on vegetation. Dense stands of emergent or submersed vegetation, by acting as a refuge and/or by reducing predator-foraging rates, mediate predator-prey interactions among aquatic insects (11, 37, 199), between fish and aquatic insects (46, 137), and between waterfowl and aquatic insects (122). In summary, the relative importance of top-down and bottom-up mechanisms in regulating wetland insect communities should vary both spatially and temporally depending on vegetation characteristics, hydroperiod, and the seasonal dynamics of predators and prey.

Succession

Above we discussed how life-history strategies affect the initial colonization of newly inundated wetlands. Here we discuss how communities subsequently change following that colonization phase. After inundation, species richness and overall density of the invertebrate community steadily increase for one to six months and then level off for that year (92, 95, 183). Densities can continue to increase during a second year of continuous flooding (101, 102). Multivoltine species that produce population peaks followed by mass emergence will cause temporary deviations in this pattern (95).

In addition to density changes, species compositions can also change (12, 42, 49, 81, 92, 95, 102). In terms of numbers, various crustacean zooplankton and dipteran larvae tend to dominate soon after inundation and are then replaced by beetles, hemipterans, mayflies, odonates, and finally macrocrustaceans and other wingless macrofauna (12, 42, 49, 81, 92, 95, 183). The initially abundant taxa are desiccation-resistant species and rapid cyclic colonizers; they are followed by permanent water species that either disperse slowly or enter the habitat through flood waters (see colonization section).

Some changes in communities reflect trophic status. Among the midges, early colonizers are often detrital feeders, followed by algal feeders, and finally predators (102); *Chironomus* midges are noted early colonizers (12, 49, 95, 102). Densities of many insect predators, as well as other predaceous wetland taxa, tend to increase the longer the wetland remains flooded (12, 49, 92, 95, 183).

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APPLIED ECOLOGY

Insects and Waterfowl Management

INSECTS CONSUMED BY WATERFOWL Invertebrates are readily consumed by waterfowl on breeding grounds and in wintering areas (47, 120). Waterfowl often congregate in habitats rich in invertebrates (96, 120). Of the insects, midge larvae and emerging adults are of most importance to ducks (10, 47, 52, 102, 120, 164), with caddisfly larvae, odonate nymphs, water beetle larvae and adults, and water boatmen comprising other important foods (10, 21, 120, 132). However, the swimming agility of some of these latter groups makes them difficult for waterfowl to catch unless densities are high (10, 87).

Large duck species typically consume the larger insect species while smaller ducks consume both large and small insect taxa (10, 120, 132). Even within an individual midge species, some ducks may consume only the larger, more mature larvae (10). This pattern is related in part to the relative coarseness of the bill lamellae among different kinds of ducks (120, 132). Thus, abundance of the larger invertebrates, rather than simply overall abundance, may be the better predictor of waterfowl foraging behavior (87), and factors that influence invertebrate size may have important management implications (7). Because waterfowl consume only certain invertebrate taxa, the common practice of classifying insects only to order or family rather than to species may be inadequate for an accurate description of the interactions between waterfowl and insects (10, 52).

MANAGEMENT OF INSECT RESOURCES Techniques to manage insect populations in waterfowl habitats are being developed. Of the habitats managed for waterfowl, insects are particularly abundant in seasonally flooded and semipermanent marshes. Midges, beetles, water boatmen, and mosquitoes can dominate the macroinvertebrate fauna of these habitats (12, 23, 49, 87, 101, 106, 122, 125, 153). In managed swamps, many insect groups are less abundant than in marshes (with the exception of certain midges), but molluskan and macrocrustacean foods can be more abundant in swamps (49, 100, 101).

Several studies have contrasted relative insect abundances among different water depths. Some of the insect taxa known to be waterfowl food items are most abundant in shallow water (95, 100, 101, 152); others flourish in deep water (13, 23, 95, 143); and still others show no significant depth preference (12, 101, 106). Even the same benthic midge species can be concentrated in deep water zones of some marshes and shallow zones of others (10). Given the mixed responses of insects to water depth, management strategies should provide a diversity of depths. Although benthic insect larvae in deep water zones may be inaccessible to dabbling ducks, they become particularly vul-

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nerable to them during emergence (164). Seasonal drawdowns also make insects in deep water more available to dabbling ducks (100, 152).

Several studies found that numbers of water boatmen, beetles, and benthic midges can be increased by mowing dense marsh vegetation (12, 13, 87, 122, 125). However, the enhanced numbers of predatory insects in mown habitats can reduce numbers of some prey (11). Rototilling (87) or herbicide treatments (169) are less desirable alternatives to mowing for reducing vegetative cover because they may harm insects.

Adding detrital food to wetlands does not seem to be an effective way to increase numbers of invertebrates for ducks (5, 125). Using fertilizer to increase algal food supplies can increase invertebrate numbers in some cases (59) but not others (123). As discussed previously, the impact of predators may reduce any response of consumers to food additions (5). Several descriptive studies suggest that reducing predation pressure on wetland insects may increase their numbers and thus benefit waterfowl (12, 69, 76, 77, 104).

Pest Management

Because of the environmentally sensitive nature of wetlands, the development of mosquito-control strategies that do not harm nontarget species has become a priority. In tidal marshes, several innovative and safe techniques to control mosquitoes are already being used (40). Unfortunately, in nontidal wetlands, mosquito control has not yet reached this level of sophistication, and pesticide applications are still the primary means of control. However, several studies indicate that natural and ecologically safe strategies could be implemented to control mosquitoes in nontidal wetlands.

In many cases, native predators effectively control mosquito populations. In temporary pools, phantom midge larvae (117), tadpole shrimp (58), or beetles (183) can control mosquitoes. In more permanent habitats, native fishes may be important mosquito predators (97). The presence of some predators may control mosquitoes indirectly by deterring mosquito oviposition (18, 58). Numbers of some predatory beetles in wetlands can be managed by manipulating vegetative cover (12, 13).

Mosquito larvae are usually associated with particular plant growth forms (149), and the cover provided by macrophytes can reduce the susceptibility of mosquito larvae to predation (136). Experimental reductions of plant cover have reduced mosquito densities (12, 13, 136, 137), and some of these manipulations also improve wetland habitats for waterfowl (12, 13). Other techniques to reduce mosquito problems while maintaining or improving habitats for wildlife are listed or reviewed by Batzer & Resh (13).

Herbivorous wetland insects may be useful for controlling noxious plants. For example, in North America, native wetland plants are being displaced by

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purple loosestrife (*Lythrum salicaria*), an exotic invader from Europe. Malecki et al (103) review an on-going coordinated effort in the United States to implement classical biological-control methodology to manage purple loosestrife using insect herbivores introduced from European wetlands.

Wetland Conservation

Drainage and water regulation can eliminate or degrade wetlands and their associated insect communities (e.g. 1, 36, 65, 91). Grazing of livestock is an additional stress on wetlands that has negative impacts on insects (74, 185). Increased sedimentation rates into wetlands from numerous anthropogenic activities may affect wetland insects indirectly by damaging wetland vegetation (85). Although some wetland insects are threatened with extinction (57, 185), insects rapidly recolonize restored wetlands (91), and the recovery of an endangered damselfly was attributed to creation of new artificial wetlands (57). In efforts to restore or preserve wetlands, insect communities are now being used by scientists as indicators of biotic integrity, particularly in Europe (1, 36, 65, 74, 91).

Pesticides in wetlands affect insects (182), and the potential loss of insect foods for wildlife is of special concern (31, 67). Some insecticides or herbicides are intentionally applied to wetlands for mosquito or pest-plant control (31, 163, 169, 172). However, many pesticides enter wetlands unintentionally via drift or run-off (45, 53, 67, 116, 186). Insecticides pose the gravest threat to wetland insects; for example, organophosphate mosquito larvicides can kill a broad spectrum of wetland insects (163). Alternatively, the microbial mosquito larvicide *Bacillus thuringiensis israelensis* has minimal impact on nontarget wetland insects (31). Although laboratory studies indicate that this insecticide can kill nontarget midge larvae, the water temperatures, water depths, and plant cover typically present in the field help protect naturally occurring midges (31). Insecticides used to control crop or forest pests can drift into wetlands and kill resident insects, particularly if they are applied aerially (53, 116, 186). Unfortunately, some of these insecticides may be unusually persistent in wetland environments (53).

Herbicides also pose a threat to wetland insects. Some herbicides are intentionally applied to wetlands to regulate plant cover or kill noxious weeds (103, 169, 172), but run-off from agriculture is a particularly serious problem (45). The primary influence of herbicides on wetland insects is indirect in that they kill the macrophytes and algae that wetland insects require (45, 172).

Neither eutrophication nor acidification of wetlands appears to strongly influence resident insects, at least directly. Introductions of massive amounts of agricultural wastewater laden with phosphorous and nitrogen into the Florida Everglades did not harm insects (144). However, those insects may eventually

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be affected indirectly as overgrowth by cattail chokes productive open-water habitats (144). Acid or acidified wetlands typically support healthy insect communities (17, 63, 77, 108, 139, 155). Apparently, many wetland insects can tolerate broad ranges of environmental pH (63, 155, 161), so they may be poor indicators of environmental stress from acid pollutants.

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Literature Cited

1. Adamek Z, Sukop I. 1992. Invertebrate communities of former southern Moravian floodplains (Czechoslovakia) and impacts of regulation. *Regul. Rivers Res. Manage.* 7:181–92
2. Adams A. 1984. Cytobiosis in Chironomidae (Diptera)—two decades on. *Antenna* 8:58–61
3. Adamus PR, Clairain EJ, Smith RD, Young RE. 1991. *Wetland Evaluation Techniques (WET),* Vol. 2, *Methodology. Wetland Res. Prog. Tech. Rep. WRP-DE–3.* US Army Corps Engineers, Waterways Exp. Stn., Vicksburg, Miss.
4. Alarie Y, Leclair R. 1988. Water beetle records from shallow pools in southern Québec (Coleoptera: Dytiscidae). *Coleopt. Bull.* 42:353–58
5. Andersson A, Danell K. 1982. Response of freshwater macroinvertebrates to addition of terrestrial plant litter. *J. Appl. Ecol.* 19:319–25
6. Anholt BR. 1994. Cannibalism and early instar survival in a larval damselfly. *Oecologia* 99:60–65
7. Armstrong DP, Nudds TD. 1985. Factors influencing invertebrate size distributions in prairie potholes and implications for coexisting duck species. *Freshw. Invert. Biol.* 4:41–47
8. Aubin A, Leblanc A. 1986. Effet des variables sur la biomasse animale de sept mares temporaires d'eau douce du Québec méridional. *Hydrobiologia* 139: 143–52
9. Bataille KJ, Baldassarre GA. 1993. Distribution and abundance of aquatic macroinvertebrates following drought in three prairie pothole wetlands. *Wetlands* 13:260–69
10. Batzer DP, McGee M, Resh VH, Smith RR. 1993. Characteristics of invertebrates consumed by mallards and prey response to wetland flooding schedules. *Wetlands* 13:41–49
11. Batzer DP, Resh VH. 1991. Trophic interactions among a beetle predator, a chironomid grazer, and periphyton in a seasonal wetland. *Oikos* 60:251–57
12. Batzer DP, Resh VH. 1992. Macroinvertebrates of a California seasonal wetland and responses to experimental habitat manipulation. *Wetlands* 12:1–7
13. Batzer DP, Resh VH. 1992. Wetland management strategies that enhance waterfowl habitats can also control mosquitoes. *J. Am. Mosq. Control Assoc.* 8:117–25
14. Bennett DV, Streams FA. 1986. Effects of vegetation on *Notonecta* (Hemiptera) distribution in ponds with and without fish. *Oikos* 46:62–69
15. Bergey EA, Balling SF, Collins JN, Lamberti GA, Resh VH. 1993. Bionomics of invertebrates within an extensive *Potamogeton pectinatus* bed of a California marsh. *Hydrobiologia* 234: 15–24
16. Berté SB, Pritchard G. 1986. The life histories of *Limnephilus externus* Hagen, *Anabolia bimaculata* (Walker) and *Nemotaulius hostilis* (Hagen)

Annual Reviews
www.annualreviews.org/aronline

(Trichoptera, Limnephilidae) in a pond in southern Alberta, Canada. *Can. J. Zool.* 64:2348–56
17. Blancher PJ, McNicol DK. 1991. Tree swallow diets in relation to wetland acidity. *Can. J. Zool.* 69:2629–37
18. Blaustein L, Kotler BP. 1993. Oviposition habitat selection by the mosquito, *Culiseta longiareolata:* effects of conspecifics, food and green toad tadpoles. *Ecol. Entomol.* 18:104–8
19. Blaustein L, Margalit J. 1994. Mosquito larvae (*Culiseta longiareolata*) prey upon and compete with tadpoles (*Bufo viridis*). *J. Anim. Ecol.* 63:841–50
20. Blois-Heulin C, Crowley PH, Arrington M, Johnson DM. 1990. Direct and indirect effects of predators on the dominant invertebrates of two freshwater littoral communities. *Oecologia* 84: 295–306
21. Botero JE, Rusch DH. 1994. Foods of blue-winged teal in two neotropical wetlands. *J. Wildl. Manage.* 58:561–65
22. Brinson MM, Lugo AE, Brown S. 1981. Primary productivity, decomposition and consumer activity in freshwater wetlands. *Annu. Rev. Ecol. Syst.* 12:123–61
23. Broschart MR, Linder RL. 1986. Aquatic invertebrates in level ditches and adjacent emergent marsh in a South Dakota wetland. *Prairie Nat.* 18:167–78
24. Bunn SE, Boon PI. 1993. What sources of organic carbon drive food webs in billabongs? A study based on stable isotope analysis. *Oecologia* 96:85–94
25. Butler MG, Anderson DH. 1990. Cohort structure, biomass, and production of a merovoltine *Chironomus* population in a Wisconsin bog lake. *J. North Am. Benthol. Soc.* 9:180–92
26. Butler MG, Miller MC, Mozley S. 1980. Macrobenthos. In *Limnology of Tundra Ponds,* ed. JE Hobbie, pp. 297–339. Stroudsburg, PA: Dowden, Hutchinson & Ross
27. Cahoon DR, Stevenson JC. 1986. Production, predation, and decomposition in a low-salinity *Hibiscus* marsh. *Ecology* 67:1341–50
28. Campeau S, Murkin HR, Titman RD. 1994. Relative importance of algae and emergent plant litter to freshwater marsh invertebrates. *Can. J. Fish. Aquat. Sci.* 51:681–92
29. Cantrell MA. 1979. Invertebrate communities in the Lake Chilwa swamp in years of high level. In *Lake Chilwa: Studies of Change in a Tropical Ecosystem,* ed. M Kalk, AJ Mclachlan, C Howard-Williams, pp. 161–73. The Hague: Junk
30. Carpenter QJ, DeWitt CB. 1993. The effects of ant mounds and animal trails on vegetation pattern in calcareous fens. *Trans. Wis. Acad. Sci. Arts Lett.* 81:23–30
31. Charbonneau CS, Drobney RD, Rabeni CF. 1994. Effects of *Bacillus thuringiensis* var. *israelensis* on nontarget benthic organisms in a lentic habitat and factors affecting the efficacy of the larvicide. *Environ. Toxicol. Chem.* 13:267–79
32. Corbet PS. 1962. *A Biology of Dragonflies.* Chicago: Quadrangle Books
33. Corbet PS. 1980. Biology of Odonata. *Annu. Rev. Entomol.* 25:189–217
34. Corbet PS. 1984. Orientation and reproductive condition of migrating dragonflies. *Odonatologica* 13:81–88
35. Corkum LD. 1984. Movements of marsh-dwelling invertebrates. *Freshw. Biol.* 14:89–94
36. Coulson JC, Butterfield JEL, Henderson E. 1990. The effect of open drainage ditches on the plant and invertebrate communities of moorland and on the decomposition of peat. *J. Appl. Ecol.* 27:549–61
37. Crowder LB, Cooper WE. 1982. Habitat structural complexity and the interaction between bluegill and their prey. *Ecology* 1802–13
38. Cuffney TF, Wallace JB. 1987. Leaf litter processing in coastal plain streams and floodplains of southeastern Georgia, U.S.A. *Arch. Hydrobiol. Suppl.* 76:1–24
39. Cyr H, Downing JA. 1988. The abundance of phytophilous invertebrates on different species of submerged macrophytes. *Freshw. Biol.* 20:365–74
40. Dale PER, Hulsman K. 1990. A critical review of salt marsh management methods for mosquito control. *Crit. Rev. Aquat. Sci.* 3:281–311
41. Danell K, Sjöberg K. 1979. Decomposition of *Carex* and *Equisetum* in a northern Swedish lake: dry weight loss and colonization by macro-invertebrates. *J. Ecol.* 67:191–200
42. Danell K, Sjöberg K. 1982. Successional patterns of plants, invertebrates and ducks in a man-made lake. *J. Appl. Ecol.* 19:395–409
43. Davies BR. 1974. The dispersal of Chironomidae: a review. *J. Entomol. Soc. South Afr.* 39:39–62
44. Delettre YR. 1989. Effect of the duration and intensity of drought on abundance and phenology of adult Chironomidae (Diptera) in a shallow temporary pool. *Arch. Hydrobiol.* 114:383–99
45. DeNoyelles F, Kettle WD, Fromm CH, Moffett MF, Dewey SL. 1989. Use of experimental ponds to assess the effect

Annual Reviews
www.annualreviews.org/aronline

of a pesticide on the aquatic environment. See Ref. 182, pp. 41–56
46. Diehl S. 1992. Fish predation and benthic community structure: the role of omnivory and habitat complexity. *Ecology* 73:1646–61
47. DuBowy PJ. 1988. Waterfowl communities and seasonal environments: temporal variability in interspecific competition. *Ecology* 69:1439–53
48. Duffy WG. 1994. Demographics of *Lestes disjunctus disjunctus* (Odonata: Zygoptera) in a riverine wetland. *Can. J. Zool.* 72:910–17
49. Duffy WG, LaBar DJ. 1994. Aquatic invertebrate production in Southeastern USA wetlands during winter and spring. *Wetlands* 14:88–97
50. Dvorák J. 1987. Production-ecological relationships between aquatic vascular plants and invertebrates in shallow waters and wetlands—a review. *Arch. Hydrobiol. Beih. Ergeb. Limnol.* 27:181–84
51. Escher RL, Lounibos LP. 1993. Insect associates of *Pistia stratiotes* (Arales: Araceae) in southeastern Florida. *Fla. Entomol.* 76:473–500
52. Euliss NH, Grodhaus G. 1987. Management of midges and other invertebrates for waterfowl wintering in California. *Calif. Fish Game* 73:238–43
53. Fairchild WL, Eidt DC. 1993. Perturbation of the aquatic invertebrate community of acidic bog ponds by the insecticide fenitrothion. *Arch. Environ. Contam. Toxicol.* 25:170–83
54. Farkas MJ, Brust RA. 1986. Phenology of the mosquito *Wyeomyia smithii* (Coq.) in Manitoba and Ontario. *Can. J. Zool.* 64:285–90
55. Finnamore AT, Marshall SA, eds. 1994. *Terrestrial Arthropods of Peatlands, With Particular Reference to Canada. Mem. Entomol. Soc. Can.* 169:1–289
56. Foote AL, Kadlec JA, Campbell BK. 1988. Insect herbivory on an inland brackish wetland. *Wetlands* 8:67–74
57. Fox AD, Cham SA. 1994. Status, habitat use and conservation of the scarce blue-tailed damselfly *Ishnura pumilio* (Charpentier) (Odonata: Coenagrionidae) in Britain and Ireland. *Biol. Conserv.* 68: 115–22
58. Fry LL, Mulla MS, Adams CW. 1994. Field introductions and establishment of the tadpole shrimp, *Triops longicaudatus* (Notostraca: Triopsidae), a biological control agent of mosquitoes. *Biol. Control* 4:113–24
59. Gabor TS, Murkin HR, Stainton MP, Boughen JA, Titman RD. 1994. Nutrient additions to wetlands in the Interlake region of Manitoba, Canada: effects of a single pulse addition in spring. *Hydrobiologia* 279/280:497–510
60. Gascon C. 1992. Aquatic predators and tadpole prey in central Amazonia: field data and experimental manipulations. *Ecology* 13:971–80
61. Gladden JE, Smock LA. 1990. Macroinvertebrate distribution and production on the floodplains of two lowland headwater streams. *Freshw. Biol.* 24:533–45
62. Goonan PM, Beer JA, Thompson TB, Suter PJ. 1992. Wetlands of the River Murray flood plain, South Australia. 1. Preliminary survey of the biota and physico-chemistry of ten wetlands from Chowilla to Mannum. *Trans. R. Soc. South Aust.* 116:81–94
63. Gorham CT, Vodopich DS. 1992. Effects of acidic pH on predation rates and survivorship of damselfly nymphs. *Hydrobiologia* 242:51–62
64. Goyer RA, Lenhard GJ, Smith JD. 1990. Insect herbivores of a bald-cypress/tupelo ecosystem. *For. Ecol. Manage.* 33/34:517–21
65. Greenwood MT, Bickerton MA, Castella E, Large ARG, Petts GE. 1991. The use of Coleoptera (Arthropoda: Insecta) for floodplain characterization on the River Trent, U.K. *Regul. Rivers Res. Manage.* 6:321–32
66. Growns JE, Davis JA, Cheal F, Schmidt LG, Rosich RS, Bradley SJ. 1992. Multivariate pattern analysis of wetland invertebrate communities and environmental variables in Western Australia. *Aust. J. Ecol.* 17:275–88
67. Grue CE, DeWeese LR, Mineau P, Swanson GA, Foster JR, et al. 1986. Potential impacts of agricultural chemicals on waterfowl and other wildlife inhabiting prairie wetlands: an evaluation of research needs and approaches. *Trans. North Am. Wildl. Nat. Res. Conf.* 51:357–83
68. Hann BJ. 1991. Invertebrate grazer-periphyton interactions in a eutrophic marsh pond. *Freshw. Biol.* 26:87–96
69. Hanson MA, Butler MG. 1994. Responses to food web manipulation in a shallow waterfowl lake. *Hydrobiologia* 279/280:457–66
70. Hanson BA, Swanson GA. 1989. Coleoptera species inhabiting prairie wetlands of the Cottonwood Lake Area, Stutsman County, North Dakota. *Prairie Nat.* 21:49–57
71. Hargeby A. 1990. Macrophyte associated invertebrates and the effect of habitat permanence. *Oikos* 57:338–46
72. Harrison RG. 1980. Dispersal polymorphisms in insects. *Annu. Rev. Ecol. Syst.* 11:95–118

Annual Reviews
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73. Henrikson BI. 1988. The absence of antipredator behaviour in the larvae of *Leucorrhinia dubia* (Odonata) and the consequences for their distribution. *Oikos* 51:179–83
74. Holmes PR, Boyce DC, Reed DK. 1993. The ground beetle (Coleoptera: Carabidae) fauna of Welsh peatland biotopes: factors influencing the distribution of ground beetles and conservation implications. *Biol. Conserv.* 63:153–61
75. Holomuzki JR, Collins JP. 1987. Trophic dynamics of a top predator, *Ambystoma tigrinum nebulosum* (Caudata: Ambystomatidae) in a lentic community. *Copeia* 1987:949–57
76. Huener JD, Kadlec JA. 1992. Macroinvertebrate response to marsh management strategies in Utah. *Wetlands* 12: 72–78
77. Hunter ML, Jones JJ, Gibbs KE, Moring JR. 1986. Duckling responses to lake acidification: do black ducks and fish compete? *Oikos* 47:26–32
78. Irmler U, Junk WJ. 1982. The inhabitation of artificially exposed leaf samples by aquatic macro-invertebrates at the margin of Amazonian inundation forests. *Trop. Ecol.* 23:64–75
79. Jackson JM, Mclachlan AJ. 1991. Rainpools on peat moorland as island habitats for midge larvae. *Hydrobiologia* 209:59–65
80. Jeffries M. 1993. Invertebrate colonization of artificial pondweeds of differing fractal dimension. *Oikos* 67:142–48
81. Jeffries MJ. 1994. Invertebrate communities and turnover in wetland ponds affected by drought. *Freshw. Biol.* 32: 603–12
82. Johansson F. 1993. Intraguild predation and cannibalism in odonate larvae: effects of foraging behaviour and zooplankton availability. *Oikos* 66:80–87
83. Johansson F, Nilsson AN. 1991. Freezing tolerance and drought resistance of *Somatochlora alpestris* (Selys) larvae in boreal temporary pools (Anisoptera: Corduliidae). *Odonatologica* 20:245–52
84. Johnson DM. 1991. Behavioral ecology of larval dragonflies and damselflies. *Trends Ecol. Evol.* 6:8–13
85. Jurik TW, Wang SC, van der Valk AG. 1994. Effects of sediment load on seedling emergence from wetland seed banks. *Wetlands* 14:159–65
86. Kaminski M, Krzysztofiak L. 1992. Intensity of invertebrate penetration of the near-shore zone of a polyhumic lake in summer. *Ekol. Polska* 40:127–44
87. Kaminski RM, Prince HH. 1981. Dabbling duck activity and foraging responses to aquatic macroinvertebrates. *Auk* 98:115–26
88. Kehr AI, Schnack JA. 1991. Predator-prey relationship between giant water bugs (*Belostoma oxyurum*) and larval anurans (*Bufo arenarum*). *Alytes* 9:61–69
89. Kok CJ, van der Velde G. 1994. Decomposition and macroinvertebrate colonization of aquatic and terrestrial leaf material in alkaline and acid still water. *Freshw. Biol.* 31:65–75
90. Krieger KA. 1992. The ecology of invertebrates in Great Lakes coastal wetlands: current knowledge and research needs. *J. Great Lakes Res.* 18:634–50
91. LaGrange TG, Dinsmore JJ. 1989. Plant and animal community responses to restored Iowa wetlands. *Prairie Nat.* 21: 39–48
92. Lake PS, Bayly IAE, Morton DW. 1989. The phenology of a temporary pond in western Victoria, Australia, with special reference to invertebrate succession. *Arch. Hydrobiol.* 115:171–202
93. Landin J. 1980. Habitats, life histories, migration, and dispersal by flight of two water beetles, *Helophorus brevipalpis* and *H. strigifrons* (Hydrophilidae). *Holarct. Ecol.* 3:190–201
94. Larson DJ, House NL. 1990. Insect communities of Newfoundland bog pools with emphasis on the Odonata. *Can. Entomol.* 122:469–501
95. Layton RJ, Voshell JR. 1991. Colonization of new experimental ponds by benthic macroinvertebrates. *Environ. Entomol.* 20:110–17
96. Lillie RA, Evrard JO. 1994. Influence of macroinvertebrates and macrophytes on waterfowl utilization of wetlands in the Prairie Pothole region of northwestern Wisconsin. *Hydrobiologia* 279/280: 235–46
97. Lounibos L, Nishimura N, Dewald LB. 1992. Predation of *Mansonia* (Diptera: Culicidae) by native mosquitofish in southern Florida. *J. Med. Entomol.* 29: 236–41
98. Luken JO, Billings WD. 1986. Hummock-dwelling ants and the cycling of microtopography in an Alaskan peatland. *Can. Field-Nat.* 100:69–73
99. Mackay RJ, Wiggins GB. 1979. Ecological diversity in Trichoptera. *Annu. Rev. Entomol.* 24:185–208
100. Magee PA, Fredrickson LH, Humburg DD. 1993. Aquatic macroinvertebrate association with willow wetlands in northeastern Missouri. *Wetlands* 13: 304–10
101. Maher M. 1984. Benthic studies of waterfowl breeding habitat in south-west-

Annual Reviews
www.annualreviews.org/aronline

ern New South Wales. I. The fauna. *Aust. J. Mar. Freshw. Res.* 35:85–96
102. Maher M, Carpenter SM. 1984. Benthic studies of waterfowl breeding habitat in Southwestern New South Wales. II. Chironomid populations. *Aust. J. Mar. Freshwater Res.* 35:97–110
103. Malecki RA, Blossey B, Hight SD, Schroeder D, Kok LT, Coulson JR. 1993. Biological control of purple loosestrife—a case for using insects as control agents, after rigorous screening, and for integrating release strategies with research. *Bioscience* 43:680–86
104. Mallory ML, Blancher PJ, Weatherhead PJ, McNicol DK. 1994. Presence or absence of fish as a cue to macroinvertebrate abundance in boreal wetlands. *Hydrobiologia* 279/280:345–51
105. McArthur JV, Aho JM, Rader RB, Mills GL. 1994. Interspecific leaf interactions during decomposition in aquatic and floodplain ecosystems. *J. North Am. Benthol. Soc.* 13:57–67
106. McCrady JW, Wentz WA, Linder RL. 1986. Plants and invertebrates in a prairie wetland during duck brood-rearing. *Prairie Nat.* 18:23–32
107. McLaughlin DB, Harris HJ. 1990. Aquatic insect emergence in two Great Lakes marshes. *Wetlands Ecol. Manage.* 1:111–21
108. McNicol DK, Bendell BE, McAuley DG. 1987. Avian trophic relationships and wetland acidity. *Trans. North Am. Wildl. Nat. Res. Conf.* 52:619–27
109. McPeek MA. 1990. Behavioral differences between *Enallagma* species (Odonata) influencing differential vulnerability to predators. *Ecology* 71: 1714–26
110. Miaud C. 1993. Predation on newt eggs (*Triturus alpestris* and *T. helveticus*): identification of predators and protective role of oviposition behaviour. *J. Zool. Lond.* 231:575–82
111. Michiels NK, Dhondt AA. 1991. Characteristics of dispersal in sexually mature dragonflies. *Ecol. Entomol.* 16: 449–59
112. Mihuc T, Toetz D. 1994. Determination of diets of alpine insects using stable isotopes and gut analysis. *Am. Midl. Nat.* 131:146–55
113. Mitsch W, Gosselink JG, 1993. *Wetlands.* New York: Van Norstrand Reinhold. 2nd ed.
114. Mizuno T, Gose K, Lim RP, Furtado JI. 1982. Benthos and attached animals. In *Tasek Bera: The Ecology of a Freshwater Swamp,* ed. JI Furtado, S Mori, pp. 286–306. The Hague: Junk
115. Morin PJ, Lawler SP, Johnson EA. 1988. Competition between aquatic insects and vertebrates: interaction strength and higher order interactions. *Ecology* 69:1401–9
116. Morrill PK, Neal BR. 1990. Impact of deltamethrin insecticide on Chironomidae (Diptera) of prairie ponds. *Can. J. Zool.* 68:289–96
117. Morrison A, Andreadis TG. 1992. Larval population dynamics in a community of nearctic *Aedes* inhabiting a temporary vernal pool. *J. Am. Mosq. Control Assoc.* 8:52–57
118. Murkin EJ, Murkin HR, Titman RD. 1992. Nektonic invertebrate abundance and distribution at the emergent vegetation–open water interface in the Delta Marsh, Manitoba, Canada. *Wetlands* 12: 45–52
119. Murkin HR. 1989. The basis for food chains in prairie wetlands. In *Northern Prairie Wetlands,* ed. AG van der Valk, pp. 316–38. Ames: Iowa State Univ. Press
120. Murkin HR, Batt BDJ. 1987. The interactions of vertebrates and invertebrates in peatlands and marshes. See Ref. 154, pp. 15–30
121. Murkin HR, Kadlec JA. 1986. Responses by benthic macroinvertebrates to prolonged flooding of marsh habitat. *Can. J. Zool.* 64:65–72
122. Murkin HR, Kaminski RM, Titman RD. 1982. Responses by dabbling ducks and aquatic invertebrates to an experimentally manipulated cattail marsh. *Can. J. Zool.* 60:2324–32
123. Murkin HR, Pollard BJ, Stainton MP, Boughen JA, Titman RD. 1994. Nutrient additions to wetlands in the Interlake region of Manitoba, Canada: effects of periodic additions throughout the growing season. *Hydrobiologia* 279/280: 483–95
124. Muthukrishnan J, Palavesam A. 1992. Secondary production and energy flow through *Kiefferulus barbitarsis* (Diptera: Chironomidae) in tropical ponds. *Arch. Hydrobiol.* 125:207–26
125. Neckles HA, Murkin HR, Cooper JA. 1990. Influences of seasonal flooding on macroinvertebrate abundance in wetland habitats. *Freshw. Biol.* 23:311–22
126. Neill C, Cornwell JC. 1992. Stable carbon, nitrogen, and sulfur isotopes in a prairie marsh food web. *Wetlands* 12: 217–24
127. Nelson JW, Kadlec JA. 1984. A conceptual approach to relating habitat structure and macroinvertebrate production in freshwater wetlands. *Trans. North Am. Wildl. Nat. Res. Conf.* 49: 262–70

Annual Reviews
www.annualreviews.org/aronline

128. Nelson JW, Kadlec JA, Murkin HR. 1990. Responses by macroinvertebrates to cattail litter quality and timing of litter submergence in a northern prairie marsh. *Wetlands* 10:47–60
129. Nilsson AN. 1986. Community structure in the Dytiscidae (Coleoptera) of a northern Swedish seasonal pond. *Ann. Zool. Fenn.* 23:39–47
130. Nilsson AN, Söderström O. 1988. Larval consumption rates, interspecific predation, and local guild composition of egg-overwintering *Agabus* (Coleoptera, Dytiscidae) species in vernal ponds. *Oecologia* 76:131–37
131. Nolte U. 1989. Observations on neotropical rainpools (Bolivia) with emphasis on Chironomidae (Diptera). *Stud. Neotrop. Fauna Environ.* 24:105–20
132. Nummi P. 1993. Food-niche relationships of sympatric mallards and green-winged teals. *Can. J. Zool.* 71:49–55
133. Oertli B. 1993. Leaf litter processing and energy flow through macroinvertebrates in a woodland pond (Switzerland). *Oecologia* 96:466–77
134. Orians GH. 1980. *Some Adaptations of Marsh-Nesting Blackbirds.* Princeton, NJ: Princeton Univ. Press
135. Orians GH, Wittenberger JF. 1991. Spatial and temporal scales in habitat selection. *Am. Nat.* 137(Suppl.):S29–S49
136. Orr BK, Resh VH. 1989. Experimental test of the influence of aquatic macrophyte cover on the survival of *Anopheles* larvae. *J. Am. Mosq. Control Assoc.* 5:579–85
137. Orr BK, Resh VH. 1992. Influence of *Myriophyllum aquaticum* cover on *Anopheles* mosquito abundance, oviposition, and larval microhabitat. *Oecologia* 90:474–82
138. Paasivirta L, Lahti T, Perätie T. 1988. Emergence phenology and ecology of aquatic and semi-terrestrial insects on a boreal raised bog in central Finland. *Holarct. Ecol.* 11:96–105
139. Parker GR, Petrie MJ, Sears DT. 1992. Waterfowl distribution relative to wetland acidity. *J. Wildl. Manage.* 56:268–74
140. Polis GA, Myers C, Holt RD. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annu. Rev. Ecol. Syst.* 20: 297–330
141. Pritchard G. 1983. Biology of Tipulidae. *Annu. Rev. Entomol.* 28:1–22
142. Pritchard G, Berté SB. 1987. Growth and food choice by two species of limnephilid caddis larvae given natural and artificial foods. *Freshw. Biol.* 18:529–35
143. Rader RB. 1994. Macroinvertebrates of the northern Everglades: species composition and trophic structure. *Fla. Sci.* 57:22–33
144. Rader RB, Richardson CJ. 1994. Response of macroinvertebrates and small fish to nutrient enrichment in the northern Everglades. *Wetlands* 14:134–46
145. Rasmussen JB. 1985. Effects of density and microdetritus enrichment on the growth of chironomid larvae in a small pond. *Can. J. Fish. Aquat. Sci.* 42:1418–22
146. Rasmussen JB, Downing JA. 1988. The spatial response of chironomid larvae to the predatory leech *Nephelopsis obscura. Am. Nat.* 131:14–21
147. Reid F, Kelley JR, Taylor TS, Fredrickson LH. 1989. Upper Mississippi Valley wetlands—refuges and moist-soil impoundments. In *Habitat Management for Migrating and Wintering Waterfowl in North America,* ed. LM Smith, RL Pederson, RM Kaminski, pp. 181–202. Lubbock: Texas Tech Univ. Press
148. Reimer G. 1991. The ecological importance of floodplains for fish at the river March (Austria). *Arch. Hydrobiol.* 121: 355–63
149. Rejmankova E, Savage HM, Rodriguez MH, Roberts DB, Rejmanek M. 1992. Aquatic vegetation as a basis for classification of *Anopheles albimanus* Weideman (Diptera: Culicidae) larval habitats. *Environ. Entomol.* 21:598–603
150. Renshaw M, Service MW, Birley MH. 1993. Density-dependent regulation of *Aedes cantans* (Diptera: Culicidae) in natural and artificial populations. *Ecol. Entomol.* 18:223–33
151. Richardson WB, Wickham SA, Threkleld ST. 1990. Foodweb response to the experimental manipulation of a benthivore (*Cyprinus carpio*), zooplanktivore (*Menidia beryllina*) and benthic insects. *Arch. Hydrobiol.* 119:143–65
152. Riley TZ, Bookhout TA. 1990. Response of aquatic macroinvertebrates to early-spring drawdown in nodding smartweed marshes. *Wetlands* 10:173–85
153. Riley TZ, DeRoia DM. 1989. Early decomposition and invertebrate colonization of nodding smartweed leaves. *Wetlands* 9:219–25
154. Rosenberg DM, Danks HV, eds. 1987. *Aquatic Insects of Peatlands and Marshes of Canada. Mem. Entomol. Soc. Can.* 140:1–174
155. Rosenberg DM, Wiens AP, Bilyj B. 1988. Chironomidae (Diptera) of peatlands in northwestern Ontario, Canada. *Holarct. Ecol.* 11:19–31
156. Roth AH, Jackson JF. 1987. The effect

Annual Reviews
www.annualreviews.org/aronline

of pool size on recruitment of predatory insects and on mortality in a larval anuran. *Herpetologica* 43:224–32
157. Rowe CL, Sadinski WJ, Dunson WA. 1994. Predation on larval and embryonic amphibians by acid-tolerant caddisfly larvae (*Ptilostomis postica*). *J. Herpetol.* 28:357–64
158. Rzoska J. 1974. The upper Nile swamps, a tropical wetland study. *Freshw. Biol.* 4:1–30
159. Schalles JF, Shure DJ. 1989. Hydrology, community structure, and productivity patterns of a dystrophic Carolina Bay wetland. *Ecol. Monogr.* 59:365–85
160. Schleuter A. 1986. The chironomid communities of permanent and temporary pools depending on water stability and leaf litter input. *Arch. Hydrobiol* 105:471–87
161. Scudder G. 1987. Aquatic and semi-aquatic Hemiptera of peatlands and marshes in Canada. See Ref. 154, pp. 65–98
162. Setälä H, Mäkelä I. 1991. *Galerucella nymphaeae* (Col., Chrysomelidae) grazing increases *Nuphar* leaf production and affects carbon and nitrogen dynamics in ponds. *Oecologia* 86:170–76
163. Siefert RE, Lozano SJ, Brazner JC, Knuth ML. 1989. Littoral enclosures for aquatic field testing of pesticides: effects of chlorpyrifos on a natural system. See Ref. 182, pp. 57–73
164. Sjöberg K, Danell K. 1982. Feeding activity of ducks in relation to diel emergence of chironomids. *Can. J. Zool.* 60:1383–87
165. Sklar FH. 1985. Seasonality and community structure of the backswamp invertebrates in a Louisiana Cypress-Tupelo wetland. *Wetlands* 5:69–86
166. Smock L, Harlowe KL. 1983. Utilization and processing of freshwater wetland macrophytes by the detritivore *Asselus forbesi*. *Ecology* 64:1556–65
167. Smock LA, Stoneburner DL. 1980. The response of macroinvertebrates to aquatic macrophyte decomposition. *Oikos* 35:397–403
168. Söderström O, Nilsson AN. 1987. Do nymphs of *Parameletus chelifer* and *P. minor* (Ephemeroptera) reduce mortality from predation by occupying temporary habitats? *Oecologia* 74:39–46
169. Solberg KL, Higgins KF. 1993. Effects of glyphosate herbicide on cattails, invertebrates, and waterfowl in South Dakota wetlands. *Wildl. Soc. Bull.* 21: 299–307
170. Deleted in proof
171. Spence JR, Anderson NM. 1994. Biology of water striders: interactions between systematics and ecology. *Annu. Rev. Entomol.* 39:101–28
172. Stephenson M, Mackie GL. 1986. Effects of 2,4-D treatment on natural benthic macroinvertebrate communities in replicate artificial ponds. *Aquat. Toxicol.* 9:243–51
173. Sternberg K. 1994. Temperature stratification in bog ponds. *Arch. Hydrobiol.* 129:373–82
174. Stiehl RB. 1994. *Habitat Evaluation Procedures Workbook.* Fort Collins, CO: Natl. Biol. Surv., Natl. Ecol. Res. Center
175. Streams FA. 1992, Intrageneric predation by *Notonecta* (Hemiptera: Notonectidae) in the laboratory and in nature. *Ann. Entomol. Soc. Am.* 85:265–73
176. Svensson BW. 1992. Changes in occupancy, niche breadth and abundance of three *Gyrinus* species as their respective range limits are approached. *Oikos* 63: 147–56
177. Tai LCC. 1967. *Biosystematic study of* Sympetrum *(Odonata: Libellulidae).* PhD thesis. Purdue Univ., West Lafayette, IN
178. Tejedo M. 1993. Size-dependent vulnerability and behavioral responses of tadpoles of two anuran species to beetle larvae predators. *Herpetologica* 49:287–94
179. Van Buskirk J. 1988. Interactive effects of dragonfly predation in experimental pond communities. *Ecology* 69:857–67
180. Van Buskirk J. 1989. Density-dependent cannibalism in larval dragonflies. *Ecology* 70:1442–49
181. Vitt D. 1994. An overview of factors that influence the development of Canadian peatlands. See Ref. 55, pp. 7–20
182. Voshell JR, ed. 1989. *Using Mesocosms to Assess the Aquatic Ecological Risks of Pesticides: Theory and Practice. Entomol. Soc. Am. Misc. Publ.* 75:1–88
183. Walton WE, Tietze NS, Mulla MS. 1990. Ecology of *Culex tarsalis* (Diptera: Culicidae): factors influencing larval abundance in mesocosms in Southern California. *J. Med. Entomol.* 27:57–67
184. Walton WE, Tietze NS, Mulla MS. 1991. Consequences of tadpole shrimp predation on mayflies in some Californian ponds. *Freshw. Biol.* 25:143–54
185. Warren MS. 1994. The UK status and suspected metapopulation structure of a threatened European butterfly, the marsh fritillary *Eurodryas aurinia. Biol. Conserv.* 67:239–49
186. Wayland M. 1991. Effect of carbofuran on selected macroinvertebrates in a prai-

Annual Reviews
www.annualreviews.org/aronline

rie parkland pond: an enclosure approach. *Arch. Environ. Contam. Toxicol.* 21:270–80
187. Werner EE, McPeek MA. 1994. Direct and indirect effects of predators on two anuran species along an environmental gradient. *Ecology* 75:1368–82
188. Whiteman HH, Wissinger SA, Bohonak AJ. 1994. Seasonal movement patterns and diet in a subalpine population of the tiger salamander, *Ambystoma tigrinum nebulosum*. *Can. J. Zool.* 72: 1780–87
189. Wiggins GB, Mackay RJ, Smith IM. 1980. Evolutionary and ecological strategies of animals in annual temporary pools. *Arch. Hydrobiol. Suppl.* 58: 97–206
190. Williams DD. 1987. *The Ecology of Temporary Waters*. Portland: Timber
191. Williams DD, Tavares-Cromar A, Kushner DJ, Coleman JR. 1993. Colonization patterns and life-history dynamics of *Culex* mosquitoes in artificial ponds of different character. *Can. J. Zool.* 71:568–78
192. Wissinger SA. 1988. Spatial distribution, life history, and estimates of larval survivorship in a 14-species assemblage of larval dragonflies (Odonata: Anisoptera). *Freshw. Biol.* 20:329–40
193. Wissinger SA. 1989. Life history and size structure of larval dragonfly populations. *J. North Am. Benthol. Soc.* 7:13–28
194. Wissinger SA. 1995. Cyclic colonization and predictable disturbance: a template for biological control in ephemeral crop habitats. *Biol. Control.* 5: In press
195. Wissinger SA, McGrady J. 1993. Intraguild predation and competition between larval dragonflies: direct and indirect effects on shared prey. *Ecology* 74:207–18
196. Wissinger SA, Sparks GB, Brown WW, Rouse GL. Intraguild predation and cannibalism among larvae of detritivorous caddisflies in subalpine ponds. *Ecology*. Submitted
197. Woodward BD, Kiesecker J. 1994. Ecological conditions and the notonectid–fairy shrimp interactions. *Southwest Nat.* 39:160–64
198. Wrubleski DA, Rosenberg DM. 1990. The Chironomidae (Diptera) of Bone Pile Pond, Delta Marsh, Manitoba, Canada. *Wetlands* 10:243–73
199. Zimmerman M, Spence JR. 1989. Prey use of the fishing spider *Dolomedes triton* (Pisauridae, Araneae): an important predator of the neuston community. *Oecologia* 80:187–94