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WETLAND ANIMAL ECOLOGY

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The ecology of wetland animals has received much less research attention than the ecology of terrestrial, aquatic, or marine animals, particularly at the community and ecosystem level. As such, relatively little ecological theory has been developed in wetland systems, and the field of wetland animal ecology tends to adapt hypotheses generated in other ecosystems. This might make sense if wetlands were viewed as hybrids or ecotones between terrestrial and aquatic/marine ecosystems. However, wetlands are not simply transitional habitats, but have unique biotic characteristics unto themselves. Plant scientists have already come to this realization, and several wetland-specific paradigms have been developed to explain ecological patterns of wetland plants (see Chapter 6). Animal researchers are just beginning to develop such paradigms.

Because wetland animal ecologists still tend to rely on work in other ecosystems, it is probably useful to frame wetland animal ecology in relation to terrestrial, aquatic, and marine systems. In terms of energy base, wetlands appear to be hybrids of terrestrial and aquatic/marine habitats (Table 7.1). Terrestrial systems are trophically based on macrophytes (grasses, forbs, shrubs, trees), aquatic and marine systems are based mostly on algae, and wetland systems are based on both macrophytes and algae. In fact, in wetlands, animal communities above the waterline probably function much like terrestrial systems, and those below the waterline function like aquatic/marine systems. However, the “terrestrial” and “aquatic” communities of wetlands are intimately interconnected.

Wetlands are often described as highly diverse and productive ecosystems. However, depending on the wetland and the animal group, this may or may not be true, at least

TABLE 7.1. Ecological Characteristics of Terrestrial, Wetland, and Aquatic/Marine Habitats

Ecological Factor	Terrestrial Forests, Grasslands	Wetland Marshes, Swamps, Seasonal Ponds	Aquatic/Marine Streams, Rivers, Lakes Near-shore Oceans
Trophic base of food webs	Macrophytes	Macrophytes, Algae	Algae
Invertebrates			
Diversity	High	Low	High
Productivity	High	Variable	High
Amphibians/reptiles			
Diversity	High	High	Low
Productivity	Variable	Variable	Low
Fish			
Diversity	—	Low	High
Productivity	—	High	High
Birds			
Diversity	High	High	Low
Productivity	High	High	Low
Mammals			
Diversity	High	Low	Low
Productivity	High	Variable	Variable

in relation to the diversity and productivity in terrestrial or aquatic/marine systems. For example, such a statement would often be erroneous for invertebrates (Table 7.1). Invertebrate diversity in wetlands is often much lower than in either terrestrial or aquatic/marine habitats, probably because of fluctuating abiotic conditions (Chapter 4). Invertebrates may be highly productive in some wetlands (seasonal ponds, marshes, tidal marshes), but in others (peatlands, swamps) productivity is typically low. In contrast, the herpetofauna (amphibians and reptiles) of wetlands is typically more diverse and productive than in either terrestrial or aquatic/marine habitats. Fish productivity in wetlands can be very high, but the diversity is typically quite low in comparison to aquatic or marine habitats. Bird diversity and production can be high in wetlands, but no more so than many terrestrial forests and meadows. While certain wetland mammals (beaver, nutria, and muskrats) are crucially important to wetland ecology, the overall diversity and productivity of mammals in wetlands is low. Overall, animal diversity and productivity in wetlands is not unusual and probably falls within the normal range of variation for ecosystems in general.

Recognizing that the ecological functions of animals in wetlands share features with the faunas of terrestrial and aquatic/marine habitats, we frame this chapter to focus



FIGURE 7.1
Mixed wetland habitats in Georgia's Okefenokee Swamp. The macrophytes in marshy areas and leaves and wood in forested areas are the most obvious energy sources for wetland animals.

on some broadly applicable principles but highlight unique aspects of wetlands. The roles of animals in food webs are probably their most important contribution to overall wetland ecosystem function, and so the initial section of this chapter focuses on animal trophic ecology. We then discuss variation in wetland animal communities, emphasizing how communities change both spatially and temporally. In the final section of the chapter, we narrow our focus and discuss the ecology of those animal populations that play especially important roles in wetland ecosystems or are of special interest to humans.

TROPHIC ECOLOGY

THE TROPHIC BASIS FOR ANIMAL PRODUCTION

A defining feature of many wetlands is the lush growth of plants such as emergent herbaceous vegetation in freshwater and estuarine marshes, and trees in freshwater swamps, mangrove swamps, and woodland ponds (Fig. 7.1). At first glance, it might seem obvious that the abundance of energy from these plants should provide the basis for wetland food webs. However, the true picture is much more complicated. Actually, an assortment of foods, including living macrophytes, detritus from macrophytes, algae, and microbes (bacteria, fungi), support populations of primary consumer animals. These foods can vary

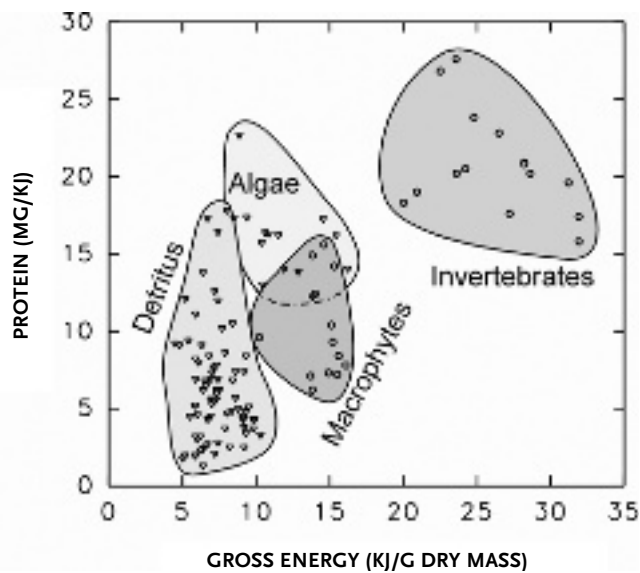


FIGURE 7.2

Relative qualities of detritus, living macrophyte tissue, and algae in terms of caloric and protein content. Figure was adapted from Bowen and associates (1995) with the permission of the senior author and the Ecological Society of America.

widely in nutritional quality (Fig. 7.2). The relative importance of each of these energy sources to overall wetland animal production fuels a continuing debate among wetland ecologists, and below we present and synthesize some diverse perspectives on this issue.

Macrophyte Herbivory

Wetland macrophytes are consumed by an assortment of herbivorous animals. In marshes, muskrats (*Ondatra zibethicus*) use emergent plants for food and to construct lodges and feeding platforms. In some cases, these rodents can consume a significant portion of the available plant biomass (Clark 2000, see below). Many species of waterfowl feed extensively on submersed aquatic plants or the seeds of emergent plants, and their grazing can impact plant-standing crops when ducks become locally abundant (Marklund et al. 2002). The explosive population increase of snow geese in the 1990s has led to the overgrazing of plant stands in tundra wetlands, possibly threatening ecosystem integrity (Kotanan and Jefferies 1997). In some estuaries, animals more commonly associated with uplands, such as hares (van der Wal et al. 1998), can be important herbivores on salt marsh plants. Also as in terrestrial habitats, insects can be important herbivores in wetlands. In salt marshes, an assortment of planthoppers feed on cordgrass (*Spartina*) and other emergent plants (Denno et al. 2002; Moon and Stiling 2002). Outbreaks of moth larvae can completely defoliate wetland trees (Goyer et al. 1990), and chrysomelid leaf beetles can consume most of the leaf production in some water lily beds (Wallace and O'Hop 1985).

Herbivorous insects (beetles and moths) are being used to biologically control invasive wetland plants (Malecki et al. 1993), which is clear evidence of the ecological importance of insect herbivores to wetlands (Blossey and Hunt-Joshi 2003). It is noteworthy that virtually all of the examples of herbivorous animals impacting macrophytes involve terrestrial animals, and that typically much of the herbivory is above the waterline. Few truly aquatic animals in wetlands seem adapted to feed on living macrophytes (Batzer and Wissinger 1996). So, in terms of macrophyte/herbivore interactions, wetland ecosystems probably function more like terrestrial forests or grasslands than like aquatic lakes or streams.

While macrophyte herbivory by terrestrial animals is clearly an important influence on wetland ecosystem function, only a handful of animal species consume living macrophytes in wetlands. Thus, the impact of herbivory is probably somewhat limited, except during population outbreaks. Even when herbivore densities are high, the vast majority of wetland plant production still is not consumed (Foote et al. 1988; Clark 2000; Marklund et al. 2002). Instead, most macrophyte tissue becomes detritus after the plants senesce.

Detritivory

If living macrophyte tissue is not the primary food base for animals in wetland food webs, the enormous influx of macrophyte detritus from annual senescence or autumn leaf fall would be a logical alternative. In fact, wetlands have been called *detritus-based ecosystems* (Odum and Heald 1975; Brinson et al. 1981). In terms of overall ecosystem function, that assessment is probably accurate because macrophyte detritus is clearly the major foundation for the microbial community (see Chapters 5 and 8). However, it has yet to be demonstrated that a substantial amount of the detrital energy cycling in the microbial loop is transformed into animal biomass. Detritus by itself is a relatively poor quality food source for animals (Fig. 7.2). Thus, the extent to which wetland animal production is based on macrophyte detritus remains an open question.

A profitable approach for assessing the relative importance of macrophyte detritus versus other sources of energy (e.g., algae) involves carbon stable isotope analysis. The carbon atom normally has an atomic weight of 12, but a small percentage (<2%) of carbon atoms naturally has an atomic weight of 13. The $^{13}\text{C}/^{12}\text{C}$ ratio differs among various plants and animals because the isotopes are assimilated, metabolized, and excreted at different rates. Working under the assumption that an animal is what it eats, the carbon isotope ratio of a particular animal should mirror the ratio in its food, and this permits researchers to match animals to their food supply. This approach has advantages over simple gut analysis because it assesses not only food consumption but also assimilation into the animal's tissues. On the other hand, stable isotope analyses is complicated by difficulties in separating isotopic signatures among similar plants (and even seasonally within a single plant species), and by difficulties in relating the isotopic signature of a generalist feeding animal to its diverse food base.

Stable isotope studies have confirmed that some animals specifically adapted to consume macrophyte detritus, such as limnephilid caddisfly shredders, do in fact derive most of their carbon from detritus (Mihuc and Toetz 1994). Furthermore, community-wide analyses in California's Tijuana Estuary (Kwak and Zedler 1997) indicated that *Spartina* detritus was the primary source of carbon for fishes, although most invertebrates and a clapper rail depended directly or indirectly on macroalgae. Currin and associates (1995, 2003) and Stribling and Cornwell (1997) also found that *Spartina* detritus was an important food to animals (fish and invertebrates) in eastern U.S. tidal marshes, although they found that other macrophyte tissue, phytoplankton, and benthic algae were equally important. Wantzen and colleagues (2002a) concluded that much of the fish community in Brazil's Pantanal was based on macrophytes. In this tropical wetland, both herbivorous and detritivorous fishes were important, and the consumption of terrestrial insect herbivores by invertivore fish channeled additional macrophyte energy into the fish community. Other studies conclude that much of the animal production in wetlands is supported by foods other than macrophyte detritus (Neill and Cornwell 1992; Bunn and Boon 1993). On the floodplain of Venezuela's Orinoco River, for instance, 98% of the available carbon exists in the lush growth of wetland grasses, water hyacinth, and floodplain trees, but the carbon isotopic signatures of most fish and invertebrates matched planktonic and epiphytic algae rather than vascular plants (Hamilton et al. 1992; Lewis et al. 2001). Bouillon and colleagues (2002) found that most benthic invertebrates in an estuarine mangrove wetland were assimilating algae over mangrove-derived detritus, a noteworthy example because mangroves are the habitats where the axiom that wetlands are detritus-based systems was first developed (Odum and Heald 1975). France (1998) also found that fiddler crabs, important consumers in tropical mangrove wetlands and traditionally considered to be detritivores, were selecting foods other than vascular plant detritus.

A powerful research approach to assess the degree to which macrophyte detritus is supporting animal production in wetlands is to manipulate detrital supplies experimentally. In a Canadian study (Murkin et al. 1982), cattail cover was reduced by cutting to 0% (control), 30%, 50%, or 70% of the original standing stock, and the plant slash was removed. Initially in the spring, invertebrate biomass was lower in the cover reduction plots, suggesting a link between animal production and detrital reductions. However, as the season progressed, invertebrate biomass steadily increased in the removal plots until it exceeded the biomass in the control plot, suggesting that some other food source supported the invertebrate production. Waterfowl use of plots mirrored invertebrate population trends, and because these birds consume invertebrates, it was suggested the birds were responding to changes in invertebrate resource levels. In a subsequent study in Canada, Neckles and associates (1990) harvested and removed the emergent vegetation from one seasonal marsh at summer's end, while they left vegetation in a second marsh undisturbed. Despite the drastic decline in detritus availability in the manipulated marsh, invertebrate composition and abundance in the two habitats the next year remained remarkably similar. Animal production in

these marshes did not appear to be detritus based. Similarly, in forested wetlands, logging is a manipulation that drastically affects detrital dynamics, with a reduction of leaf-fall inputs being a conspicuous loss. Although logging can alter animal community compositions, overall animal production in affected wetlands typically either remains similar or increases, instead of declining (Hutchens et al. 2004). In summary, experimental evidence that wetland animal production is based primarily on detritus is lacking.

To assess the trophic basis of animal production, we may need to readjust our thinking about wetlands. While accepting that the majority of energy cycling through wetlands passes through the detrital pool, it appears likely that much of the energy for wetland animals is being derived from other sources. Because macrophyte detritus is a poor-quality food relative to living macrophytes or algae both in terms of caloric and protein content (Fig. 7.2), relatively few wetland animals may be able to use macrophyte detritus as their primary food source despite its abundance. This might explain why many, if not most, detritivorous animals supplement their diets with algae (Mihuc 1997) and/or animal material (Wissinger et al. 2004b).

Before completing our discussion on the interactions of wetland animals and detritus, we should assess the impacts of animals on detrital decomposition. In streams, insect shredders are crucially important to detrital decomposition because they convert coarse particulate organic matter (e.g., leaves, wood) into smaller particles that can be utilized by other consumers (Table 7.2 describes some different functional feeding groups, including shredders). Although this concept has not been as well developed in wetland systems, similar scenarios may develop in some salt marshes and freshwater wetlands. Newell and Barlöcher (1993) estimated that when populations of the salt marsh periwinkle (*Littoraria irrorata*) were high, the snails could remove 2% to 3% of the available biomass of dead salt marsh cordgrass *Spartina* leaves from Georgia salt marshes daily. In a subsequent study in that ecosystem, Graca and associates (2000) found that an amphipod crustacean also consumed large amounts of decaying *Spartina* leaves, and their feeding stimulated fungal production on the remnant leaves. In a freshwater macrocosm experiment (Fazi and Rossi 2000), decay rates of alder leaves increased as densities of invertebrate shredders and scrapers increased. Oertli (1993) assessed leaf-litter processing and energy flow through macroinvertebrates in a woodland pond and attributed 11.2% of the breakdown of oak leaves to invertebrate shredders. Where shredding animals are abundant, they probably play important roles in decomposition. However, shredding organisms are rare in many wetlands, and degradation of detritus may instead occur through microbial and physical processes (Cuffney and Wallace 1987; Oertli 1993; Wissinger 1999; Batzer et al. 2005). Compared with the detailed knowledge about the relative roles of invertebrates, fungi, bacteria, and physical processes to litter decomposition in streams (e.g., Hieber and Gessner 2002), there is a surprising dearth of primary evidence from wetland ecosystems.

TABLE 7.2. Functional Feeding Groups (FFG)

FFG	Ingestion Method and Food Resource	Wetland Examples
Shredders	Shred living plants or plant detritus (leaves, wood)	Caddisfly larvae Muskrats
Collectors		
Gatherers	Collect small food items from surfaces	Midge larvae Dabbling ducks
Filterers	Collect small particles (algae, bacteria, protists, detritus) from water	Fingernail clams Mosquito larvae Spoonbill ducks
Scrapers	Scrape algae or biofilms from surfaces	Snails Frog tadpoles
Predators	Engulf animal prey	Dragonfly nymphs Salamanders Fish Herons
Piercers ^a	Suck fluids from plants or animals	Water bugs Plant bugs

^aThis category is not commonly used by researchers, and piercing predators (e.g., water bugs) are often lumped together with engulfing predators.

NOTE: Adapted from Cummins (1973).

Algal Herbivory

In the stable isotope studies discussed previously, the importance of algae to wetland food webs, relative to detritus, was a common theme. Stable isotope studies from an assortment of wetland types implicate algae as a particularly important energy base for food webs, including mangroves (France 1998; Bouillon et al. 2002), salt marshes (Currin et al. 1995, 2003; Kwak and Zedler 1997; Stribling and Cornwell 1997; Dittel et al. 2000; Herman et al. 2000), tidal mudflats (Melville and Connolly 2003), river floodplains (Hamilton et al. 1992; Lewis et al. 2001; Herwig et al. 2004), freshwater marshes (Neill and Cornwell 1992; Bunn and Boon 1993; Keough et al. 1998), and inland saline marshes (Hart and Lovvorn 2003). Most of these papers contain statements to the effect that the conventional wisdom of wetland food webs being based on macrophyte tissue needs to be reevaluated, and the importance of planktonic, benthic, and/or epiphytic algae needs to be more fully recognized.

Although this body of descriptive evidence points toward the importance of algae to animals in wetland food webs, few studies have evaluated relationships experimentally. However, those that have been conducted suggest a tight linkage between algae and wetland invertebrates. In an oligotrophic marsh in central Canada, separate studies by Campeau and associates (1994) and Gabor and colleagues (1994) both found that stimulating algal

biomass through experimental nutrient enrichment increased invertebrate densities. Rader and Richardson (1994) found the same bottom-up “cascade” in the Florida Everglades, where nutrient enrichment from agriculture increased growth of algae and in turn invertebrates and small fish. Even in the absence of nutrient enrichment, a tight link between algae and invertebrates was suggested by studies in a permanent marsh in Manitoba (Hann 1991) and a seasonal marsh in California (Batzer and Resh 1991), where microcrustacean and/or midge grazers reduced algal biomass to very low levels. Because algae-consuming invertebrates are in turn consumed by predatory invertebrates, fish, and birds, the microscopic algae become a crucial foundation of wetland food webs.

One reason that algae might be overlooked in food web studies is that turnover rates are high, and standing crops are kept low by grazing; hence, algae are not as visually obvious to researchers as are macrophytes. The tendency of researchers to focus on resources that are abundant may be a flawed strategy when assessing food web interactions in wetlands because the abundance of a resource may simply suggest that few consumers eat that material. In contrast, those foods that support consumers are rapidly consumed and therefore might occur at low-standing stocks. (By analogy, if someone were trying to assess the diets of four-year-old children by what is left on their dinner plates, one might come to assume that they live primarily on vegetables.) While algal standing crops may be kept low by grazers at any one point in time, algae grow very rapidly, and this productivity may be sufficient to support much of the animal secondary production in wetlands (Lewis et al. 2001). Grazing can actually enhance productivity of algal periphyton in streams because only actively growing surface films remain (Lamberti and Resh 1983), but whether that relationship exists in wetlands has not been explored. Not all wetland algae, however, are palatable to consumers. While benthic, epiphytic, and planktonic algae are all believed to be important foods, floating beds of filamentous green algae (called *metaphyton*) are not consumed to any great extent (Neill and Cornwell 1992; Mihuc and Toetz 1994), which might explain why beds of metaphyton are able to develop in the first place. Hart and Lovvorn (2003) found that many organisms find amorphous detritus derived from algae to be a nutritious food but do not consume living algae.

It has been proposed that algae and detritus are not entirely separate entities in terms of carbon transfer to wetland animals (Wissinger 1999). Keough and associates (1998) suggest that algae can fix dissolved carbon derived from decomposing detritus, and so algae may serve as an indirect link between wetland detritus and animals.

Synthesis of the Trophic Basis for Wetland Animal Production

In Figure 7.3, we attempt to synthesize existing knowledge on the basis of wetland food webs. Living macrophytes are consumed by several herbivores, of which terrestrial animals such as muskrats, moth and beetle larvae, and waterfowl are particularly notable. However, most macrophyte tissue is not consumed and instead enters the detrital pool. Relatively few animals can directly consume plant detritus, probably because nutritionally this material is a poor-quality resource (Fig. 7.2). Most wetland detritus is probably

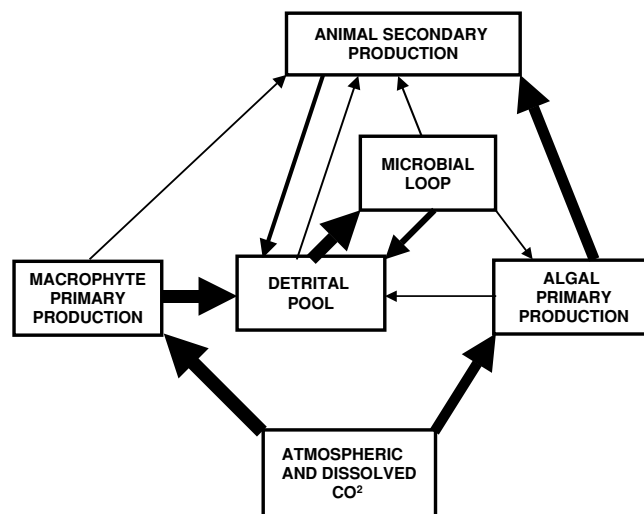


FIGURE 7.3

Schematic showing how animal secondary production in wetlands is based trophically on carbon from living macrophytes, detritus, and algae, with the link with algae being particularly strong.

consumed by the microbial community rather than animals. The extent to which the microbial community transfers energy from detritus to animals is not known. Rather than living or dead macrophytes, most evidence to date points toward algae as serving as the primary base of wetland food webs. Of course, exceptions to this general scheme will exist. For example, forested wetlands are shaded, and under restricted light conditions algal production will be reduced. Forested wetlands are probably detritus based, although algal production during leaf-off periods may still be important.

Why is it important to establish which energy sources are the foundation of food webs? If wetland food webs are based on living plants or detritus, it seems less likely that animal populations or communities will become food limited because of the enormous volume of these foods available in most wetlands. By contrast, if wetland trophic structure is algal based, food limitation is more likely to develop because the amount of algal biomass—especially the palatable planktonic, benthic, and epiphytic forms—available for wetland animal consumption is typically small (perhaps because animals compete intensively for this resource). Understanding the functional basis of wetland food webs will allow us to better predict consequences of habitat alterations.

PREDATION

The animal community in many wetlands is dominated by predators. Within the aquatic invertebrate community, predatory forms such as dragonflies, aquatic beetles, true bugs, and spiders abound, more so in wetlands than in aquatic habitats (e.g., lakes, rivers, or

streams). Wetland reptiles, with the exception of some turtle species, are almost exclusively predaceous, and wetland fish (large or small) are mostly predaceous, typically on aquatic invertebrates or other fish. Adult and larval salamanders, and adult frogs and toads are all predators. While most frog larvae are considered algivores, predatory behavior by them is now known to be common (Petranka and Kennedy 1999). Among the birds, wading and shore birds prey on fish or invertebrates, and most songbirds in wetlands consume insects. Even those birds that are typically considered herbivores, such as dabbling ducks (mallards, teals), feed extensively on invertebrates when they require protein-rich food sources, especially while they are young ducklings, during feather molts, or when preparing for migration and nesting (Baldassarre and Bolen 1994).

Impacts of Predation

Predation can be a pervasive influence on wetland animal communities. In tidal mudflats and other temporary wetlands, such as drawdown impoundments, shorebirds (Order Charadriiformes) can form large flocks that have been shown via enclosure experiments to have a huge impact on benthic invertebrates. For example, Weber and Haig (1997) found that spring-migrating shorebirds reduced invertebrate abundance and biomass by about 50% but that impacts of predation varied spatially. Because shorebird flocks tend to feed in areas of highest invertebrate abundance, they proposed that a negative feedback loop existed that would tend to even out prey and predator distributions. However, they found only partial support for such a mechanism. Mercier and McNeil (1994) found a large temporal effect of the influence of shorebird predation on invertebrate numbers in overwintering habitats of Venezuela. Probably the largest effect of shorebird predation is exhibited by staging birds prior to migration, when concentrations in excess of one million birds have been observed (Wilson 1989).

Predation is also an important influence on birds themselves. Nest predation is the major cause of nest failure in most birds (Ricklefs 1969). Recent evidence implicates nest predation as a crucially important factor regulating certain waterfowl populations, especially in those associated with prairie potholes of North America, which are increasingly destroyed or fragmented from agricultural encroachment (Greenwood et al. 1995). Similarly, nest predation limits songbird populations (Sherry and Holmes 1995). In wetlands, nests built over water commonly are afforded increased protection from many nest predators compared with similar nests built over dry land. However, when a large area such as a river floodplain is inundated, some nest predators such as rat snakes and raccoons are capable of living an arboreal existence, and nest predation may actually increase in canopy nests at such times (Mullin et al. 2000). Birds such as Acadian Flycatchers (*Empidonax vireescens*) may choose nest sites that minimize access by such predators (Wilson and Cooper 1998; Mullin and Cooper 2002).

Impacts of predation can ripple throughout wetland communities. After predaceous fish (bluegill, yellow perch, bullhead) became established in Lake Christina, a shallow waterfowl lake in Minnesota, water turbidity increased, submersed macrophyte beds declined,

and benthic invertebrate populations became low (Hanson and Butler 1994a, 1994b). A wetland that historically had been a crucial feeding and staging area for migrating diving ducks no longer attracted significant bird numbers. In an effort to rehabilitate the habitat for waterfowl, fish were eliminated from the lake in 1987 using rotenone pesticide. In the first year after the fish kill, large cladocerans (*Daphnia*) became abundant, and phytoplankton populations declined (Hanson and Bulter 1994b). Water transparency increased and submersed macrophyte beds expanded, as did benthic macroinvertebrate populations. With the increased availability of plant and invertebrate foods, use by migrating ducks increased dramatically. In this wetland lake, both lower and higher trophic levels were being affected by fish predation.

In salt marshes of the southeastern United States, a snail grazer (the periwinkle, *Littoraria irrorata*) has the potential to virtually eliminate stands of cordgrass (*Spartina*). However, Siliman and Bertness (2002) found that a trophic cascade operates in these marshes where predators (blue crabs, *Callinectes sapidus*, and diamondback terrapins, *Malaclemys terrapin*) limit populations of the periwinkles, preventing them from causing large-scale defoliation of the cordgrass. They suggest that some recent massive die-offs of cordgrass in the eastern United States might have developed because humans are overharvesting predatory blue crab, permitting periwinkle populations to explode. Batzer and Resh (1991) describe a similar trophic cascade in a California seasonal wetland. When densities of predatory beetle larvae were high, they found that predation kept densities of midge grazers low, and in the absence of grazers, biomass of algal periphyton accumulated. On the other hand, if beetle densities were low, midge populations exploded, and their grazing largely eliminated the algal periphyton. Once algae were gone, the midge populations crashed, presumably from lack of food.

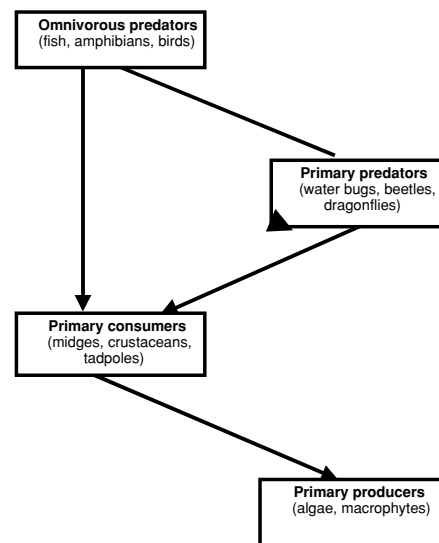
Flocking shorebirds feeding in tidal mudflats have been shown to exert indirect trophic-level effects on invertebrates by either altering competition (Kent and Day 1983; Wilson 1989) or by feeding on predators of the invertebrates (Daborn et al. 1993). In the latter example, shorebirds fed on a grazing amphipod (*Corophium volutator*), which controlled the siliceous benthic diatoms that were responsible in part for maintaining sediment cohesion. With the arrival of the migratory birds, grazing pressure on the diatoms decreased, and sediment strength increased.

Bottom-up Versus Top-down Control of Animal Populations

While every animal is influenced trophically from below by its food supply and most animals are concurrently influenced from above by predation, few studies have assessed the relative importance of each force or the interactions between bottom-up and top-down forces. Denno and colleagues (2002) used cage experiments with planthoppers in *Spartina* cordgrass stands to investigate the relative magnitude of two bottom-up forces, plant nutrition and plant structural complexity, and a top-down force, wolf-spider predation. They found that the relative influence of wolf-spider predation on planthoppers was greatest when plant condition was poor and plant thatch was present, typical of high marsh conditions. If the plants were nutritious and were lacking thatch, typical of low marsh

FIGURE 7.4

Direct and indirect pathways of predation in aquatic food webs of wetlands. Direct suppression of one trophic level by predation can result in an indirect enhancement of a second even lower trophic level, creating a trophic cascade. However, this indirect enhancement can be counterbalanced by any direct negative impacts of an omnivorous predator. The relative strengths of direct and indirect pathways of omnivory will determine the ultimate impact on a more basal species.



conditions, planthoppers were not limited by wolf-spider predation. The success of planthoppers in low marsh conditions was attributed to the insects' high growth rates, which permitted them to overwhelm any losses from predation, and mobility, which permitted them to evade capture in relatively open thatchless conditions.

Diehl (1992) also found that the structural complexity of aquatic plant stands affected the outcome of fish predation. He manipulated densities of predatory perch (*Perca fluviatilis*) in Swedish habitats with and without submersed vegetation and examined the responses of the invertebrate community. The perch were omnivorous, feeding both on predatory and nonpredatory invertebrates. Where submersed vegetation was present, perch foraging efficiency was reduced, and large predatory invertebrates were able to coexist with the fish (suggesting that habitat complexity should also be considered when modeling the effects of fish). No perch effect was evident on the populations of herbivorous and detritivorous invertebrates. However, Diehl attributed the lack of consumer response to the fact that when perch efficiency declined, the impacts of invertebrate predation probably increased. The effects of predation from fish and invertebrates counterbalanced. Because omnivorous predators (those that feed on more than one trophic level) can have both direct negative effects and indirect positive effects on lower trophic levels (Fig. 7.4), impacts on the overall food web can be complex.

Batzer (1998) found that chironomid midges in a New York marsh were also being affected by both top-down and bottom-up influences, although in this case, the bottom-up interaction from plants was nutritional rather than structural. Cage experiments were conducted where the density of large or small fish (bullheads or carp) was controlled and the biomass of cattail (*Typha*) litter was manipulated. Reducing small fish numbers and supplementing litter simultaneously enhanced densities of midges, although midge response to litter was less dramatic than the response to fish.

In wetland forests, the relative importance of top-down and bottom-up processes is not known. By comparison, in terrestrial forests, herbivorous insects are the major herbivores by biomass, and a trophic cascade involving insectivorous birds, herbivorous insects, and trees has been identified. Marquis and Whelan (1994) found increased numbers of caterpillars, increased leaf damage, and decreased productivity by saplings inside cages compared with exposed saplings, suggesting a top-down process. However, Forkner and Hunter (2000) mediated bird predation pressure in another enclosure study by manipulating nutrient levels, suggesting that the relative strength and expression of bottom-up versus top-down forces probably vary spatially in terrestrial forest systems. A similar situation probably exists for trophic relationships in floodplain forests, but spatial variation is likely complicated further by temporal variation in flooding. However, this is mere conjecture, since these sorts of trophic cascades have yet to be studied in floodplain forests. It seems likely that both top-down and bottom-up forces are operating in most habitats, but the mechanisms and outcomes of these interactions will vary spatially and temporally.

Predator/Permanence Models

In wetlands and lakes, predation is considered one of the most important forces shaping overall aquatic animal communities. The predator/permanence model developed by Wellborn and associates (1996) (modification shown in Fig. 7.5) proposes that animal communities are structured by two habitat transitions:

1. A permanence transition between temporary and permanent water habitats, and
2. A predator transition between habitats with and without fish.

Because the physical transition in permanence often covaries with the biotic transition in top predators (fish), it is difficult to infer the relative importance of the two conditions along predator-permanence gradients from comparative data alone. Habitat drying is a stress that many aquatic organisms can not tolerate, and thus temporary water habitats are inhabited only by organisms adapted to cope with desiccation (e.g., small invertebrates with rapid development; see Chapter 4). A wider range of organisms can successfully live in permanent water habitats. In permanent habitats (lakes and ponds), Wellborn and colleagues (1996) maintained that the presence or absence of predatory fish is the primary factor influencing animal communities. In permanent water habitats without fish (e.g., ponds geographically isolated from fish-bearing water, winterkill lakes), aquatic predators other than fish, such as large invertebrates or amphibians, are positioned at the top of aquatic food webs. In habitats with fish, populations of larger invertebrates and amphibians are reduced or eliminated by fish, and the invertebrate community becomes dominated by small-bodied, sessile forms that are less susceptible to fish predation.

Although the predator/permanence model is a valuable tool because it focuses attention on the importance of hydrology and fish predation, many wetlands do not fit

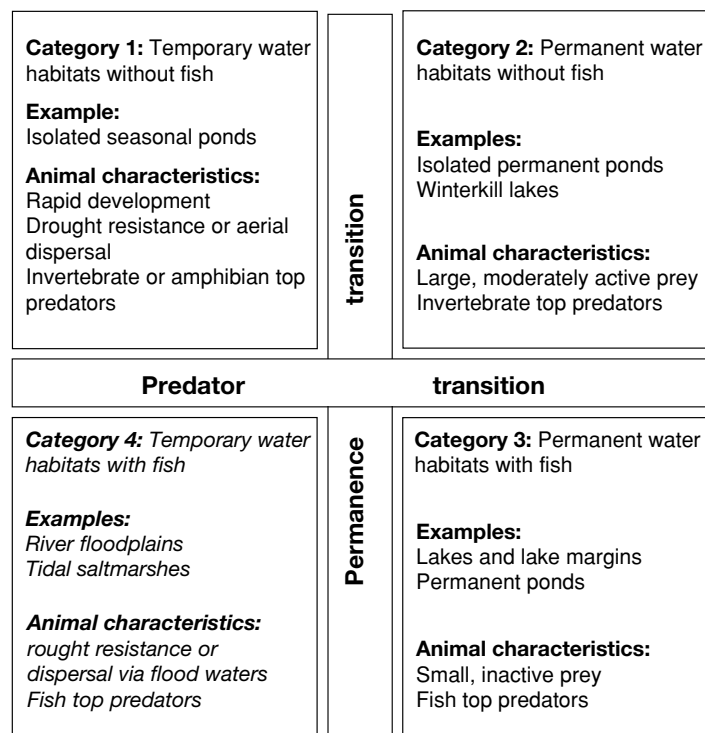


FIGURE 7.5

Permanence/predator gradients. Habitat Categories 1, 2, and 3 follow Wellborn and associates (1996), and Category 4 represents our modification of that model.

neatly into the three designated habitat categories designated by Wellborn and colleagues (1996):

1. Temporary water habitats;
2. Permanent water habitats without fish; and
3. Permanent water habitats with fish.

For example, some wetlands take on different characteristics over time. During a dry climatic cycle, a wetland might be a temporary habitat, but during a wet cycle, it may take on the character of a permanent water habitat without fish. Even if fish newly enter a wetland, it may take years before they become numerous enough to be functionally important and begin influencing overall community structure. Many wetlands actually fit into a fourth category (Fig. 7.5): temporary water habitats with fish (Kohler et al. 1999), of which floodplains or tidal marshes are good examples. These habitats are only temporarily inundated, but flood waters often contain fish. Presumably, animals inhabiting them must cope with both drying and fish predation. The permanence/predator model of Wellborn and colleagues (1996) also assumes that fish will exclude large active invertebrates via size-based prey selection

because fish are bigger than the other aquatic animals. While this may be true in lakes, the fish in many wetlands are small bodied (small minnows, topminnows, pygmy varieties, immatures of larger taxa), and they often are of similar size to invertebrates. These small fish may not be able to exclude large invertebrates, and the two groups may coexist. For example, Georgia's Okefenokee Swamp teems with fish, but most are small species (Freeman and Freeman 1985); this wetland complex also supports a plethora of large-bodied invertebrate predators (Kratzer 2002). Zimmer and associates (2000) found that fathead minnows affected densities of most invertebrates in prairie wetlands but did not affect invertebrate size distributions, suggesting that size-based selection of prey was not occurring. The Wellborn model also does not address amphibian predation, which can be very important in wetlands. In high elevation fishless wetlands of Colorado, Wissinger and associates (1999a) found that invertebrate community structure was minimally influenced by physico-chemical variables, and instead, the presence or absence of predaceous salamanders exerted the most control on invertebrates. Perhaps expanding the predator/permanence paradigm (Fig. 7.5) to include amphibians will provide additional explanatory values.

COMMUNITY ECOLOGY

SECONDARY SUCCESSION

Succession is a change in community composition over time. Primary succession occurs after a new habitat is created, and a wetland example would be the slow conversion of a glacially created shallow lake into an herbaceous marsh, then a forested wetland, and ultimately an upland (see Chapters 3 and 6). Surprisingly, changes in animal communities along primary succession gradients have yet to be described. Secondary succession occurs after an established habitat is affected by fire, a weather event, or some other disturbance. For wetland animals, most research focus on succession has been on secondary processes that occur postdisturbance.

Drought Recovery

The response of animals in drought-affected wetlands of the North American Prairie (summarized in Murkin et al. 2000) is probably the best documented case of secondary succession for wetlands. (Details on plant responses can be found in the Chapter 6 section on prairie potholes.) In the prairie pothole region, wet and dry precipitation periods tend to cycle every few decades. During dry periods, water levels in wetlands can decline dramatically, and many prairie wetlands are dewatered, exposing the habitat bottom. This first stage of the wet-dry cycle is called the *dry marsh phase* (Fig. 7.6). As wetlands dry, aquatic animals must leave the wetlands, employ some sort of drought resistance strategy (see Chapter 4), or perish. Shore and wading birds will flock to drying wetlands to feed on newly exposed or stranded aquatic invertebrates and fish. Once the wetland dries, a dramatic botanical change occurs as seeds in the seed bank germinate and begin to grow (see Chapter 6). Certain birds

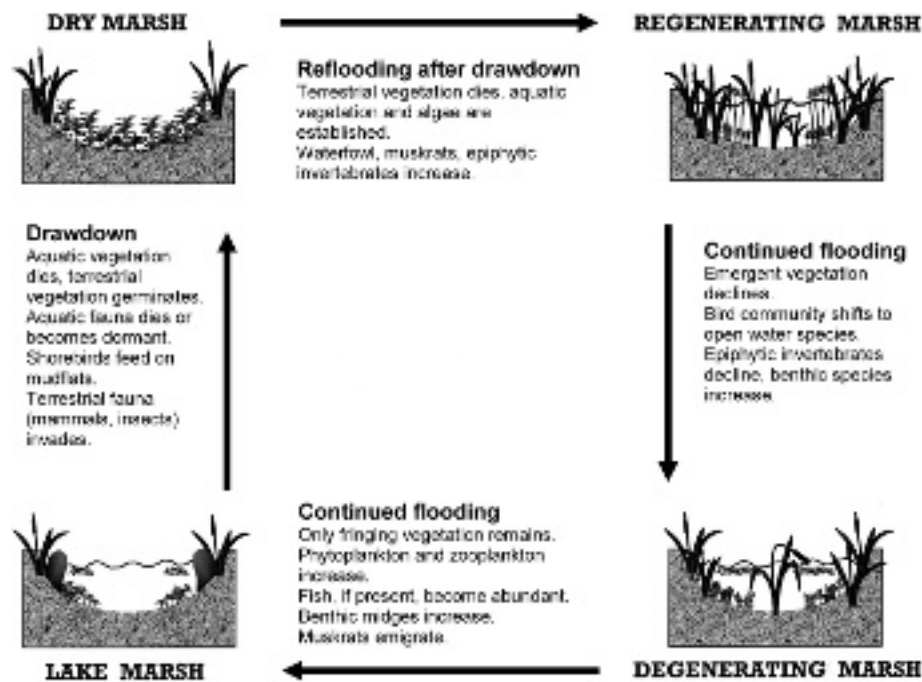


FIGURE 7.6

Successional trajectory of marsh habitats in response to periodic drying and prolonged reflooding in northern prairie marshes of central North America. Adapted from Murkin and Ross (1999), and portions reprinted with permission of John Wiley & Sons, Inc.

such as red-winged blackbirds find plant stands in dry marsh to be optimal nesting habitats (Murkin and Caldwell 2000), and the new growth of annual plants serves as food for an assortment of terrestrial herbivores (deer, insects).

Once sufficient rains return, wetlands refill, and the *regenerating marsh phase* begins (Fig. 7.6). Annual plants that germinated during the dry phase will die from flooding, whereas perennial emergent hydrophytes (sedges, reeds, cattails) expand. Submersed pondweeds that had disappeared in the dry phase become reestablished (see Chapter 6). Flooding forces the terrestrial fauna to vacate the wetland, but the wetland becomes recolonized by aquatic animals, emerging from dormancy or migrating back from surrounding wetlands. Aquatic invertebrate and amphibian populations can explode because an abundance of food and structure exists in the form of drowned annual plants and algae. Copious growth of algal food is stimulated by nutrients released from oxidized sediments and decaying vegetation (see Chapters 5 and 8). In the early stages of regeneration, invertebrate and amphibian populations will not yet be limited by predators (fish, large invertebrates), which are generally slower to reestablish. Dabbling ducks (mallards, teals) are especially attracted to the hemi-marsh conditions (roughly equal proportions of open water and plant cover) that develop during regeneration.

Regeneration usually lasts from three to five years. If flooding continues beyond that period, the *degenerating marsh phase* begins (Fig. 7.6). Stands of emergent plants will begin to thin as herbivores (muskrats, insects), disease, and the direct effects of prolonged flooding take their toll. Periods of unusually deep water that over-top emergent plants can magnify plant mortality. Minimal plant germination will occur under flooded conditions, so plants that die are not replaced, and the marsh begins to convert to a more open water condition. Aquatic invertebrates that live on plant surfaces (epiphytic forms) will decline with the loss of substrate, but invertebrates that live on mud substrates (benthic forms) may increase (Wrubleski 1999). Similarly, the avian community changes to one that prefers open water conditions (diving ducks, coots) (Murkin and Caldwell 2000). If fish occur, prolonged flooding will allow their populations to grow, and fish predation will begin shaping the overall animal community (see Fig. 7. 5). If emergent vegetation disappears from all but the fringes of the wetland, an extreme form of degeneration develops called the *lake marsh phase* (Fig. 7.6). The animal community of lake marsh will be dominated by a few species that thrive in open water (planktonic crustaceans, benthic midges, fish, piscivorous and planktivorous birds). Lake marsh will persist until another dry cycle dewateres the site, and then the cycle will repeat.

Because dabbling ducks, which are highly sought after by hunters, prosper during the earlier stages of the wet-dry cycle, many managers of wetlands use water control techniques to keep the wetlands in that condition. For example, moist-soil management is practiced on most wildlife management areas (Fredrickson and Taylor 1982). Moist-soil impoundments are dried and flooded yearly to stimulate growth of annual plants such as smartweed (*Polygonum*) and beggartick (*Bidens*) because these plants produce copious seed that is prime duck forage. Dense populations of aquatic invertebrates, especially midge larvae, develop in these newly flooded wetlands, and they are also highly desirable duck food. A second strategy used commonly to manage wetlands for waterfowl is called *semipermanent flooding*. This technique involves dewatering the wetland for a year or at least a summer season and then maintaining flooded conditions for the next three to five years. This kind of management maintains the wetland in the regenerating phase, which creates the hemi-marsh conditions preferred by many dabbling ducks, and it prevents the marsh from moving from regeneration into degeneration.

Conversion of Herbaceous Marsh to Forested Swamp

Some, but by no means all, herbaceous marshes will follow a successional trajectory toward becoming a forested wetland. This very slow process is difficult to track scientifically, and thus limited information is available on animal succession. However, clear differences in amphibian species composition exist between open and wooded wetlands. In a long-term comparative study in Michigan, species that dominated open habitat temporary wetlands such as toads (*Bufo americanus*), treefrogs (*Hyla versicolor*), green frogs (*Rana clamitans*), leopard frogs (*Rana pipiens*), and newts (*Notophthalmus viridescens*) have been replaced by wood frogs (*Rana sylvatica*), and two ambystomatid salamanders (*Ambystoma*

maculatum and *A. laterale*) as canopies have closed during forest succession (Skelly et al. 1999). The underlying mechanisms that control species shifts along canopy gradients are likely to be a combination of changes in dissolved oxygen, variation in food resources (both detrital and algal), and temperature (Werner and Glennemeier 1999; Skelly et al. 1999; Freidenburg and Skelly 2004).

More information about animal response to the conversion of marsh to swamp is available by studying the reverse process, the often rapid conversion of forested swamp into herbaceous wetland. A forested wetland can be converted naturally to an herbaceous state by fire, beaver activity, or other natural disturbances, but most documented instances of such change involve the human logging of forested wetlands. Removal of shade trees from wetlands opens up the forest floor to sunlight, which stimulates the growth of herbaceous plants and algae, and causes the formerly forested wetlands to take on the floristic characteristics of marshes (Perison et al. 1997; Gale et al. 1998) or wet meadows (Mitchell et al. 1995; Roy et al. 2000). Because the nature of the plant community influences the structure of the animal communities (Wigley and Roberts 1994), the former forested fauna dominated by salamanders, arboreal reptiles, and interior forest birds is replaced by a marsh or meadow fauna dominated by frogs, ground-dwelling reptiles, and edge- and meadow-nesting birds (Clawson et al. 1997; Hurst and Bourland 1996; Moorman and Guynn 2001; Phelps and Lancia 1995; Perison et al. 1997). There may be no overall decrease in animal species richness or diversity when a forested wetland is converted to an herbaceous wetland, but the nature of the animal community clearly changes. Presumably, if herbaceous wetlands undergo natural succession into forested wetlands, the animal community will also revert back into a typical forested fauna.

BIOGEOGRAPHY

Many wetlands occur almost as isolated habitat islands in an upland sea, and thus wetland researchers (e.g., Ebert and Balko 1987; Hall et al. 2004) have attempted to adapt tenets of the equilibrium theory of island biogeography (*sensu* MacArthur and Wilson 1967) to wetlands. MacArthur and Wilson (1967) postulated that for oceanic islands, an equilibrium develops between the immigration of new species and the extinction of those already present, and the equilibrium number of species is determined by (1) a distance effect (islands near a mainland source of species will be colonized by more species than those islands farther removed) and (2) an area effect (extinction rates on small islands will be greater than on larger islands) (Fig. 7.7). The issues of habitat size and isolation implicit in island biogeography seem likely to have application for isolated wetlands. However, some aspects of the theory will not apply to wetlands. Wetlands differ from islands in that there is seldom a single "mainland" source of species to colonize them. Further, many animals (birds, amphibians, insects) are transient residents of wetland habitats, moving between a specific wetland and other habitats to reproduce, develop, forage, seasonally migrate, or diapause.

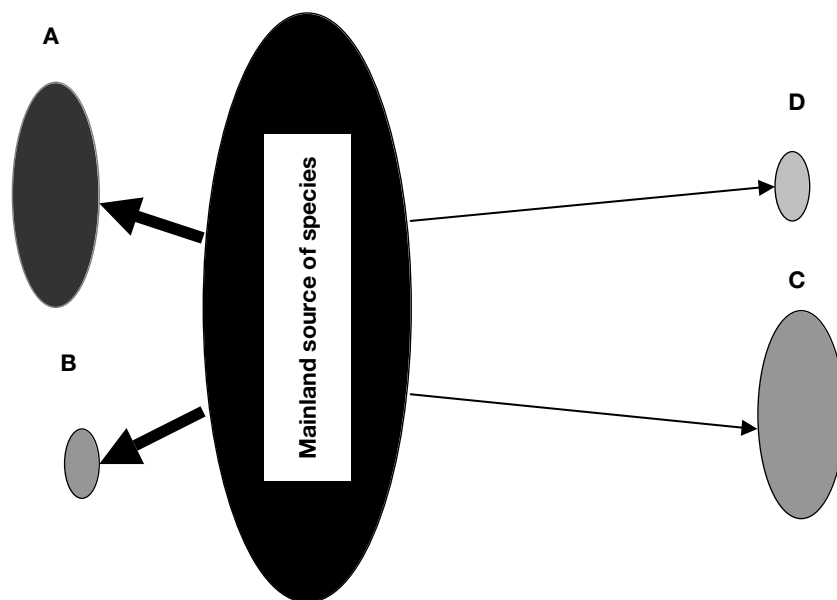


FIGURE 7.7

Adapting the equilibrium theory of island biogeography to isolated wetlands. The theory postulates that islands, and presumably isolated wetlands, close to a mainland source of species will be colonized by more species than islands farther removed from the mainland. Arrows represent this colonization and the width of the arrows the amount of colonization. The theory further postulates that extinction rates on small islands will be greater than on large islands. Thus, a large island in close proximity to the mainland will have numerous species (hence, the dark shading of island A), while a small island far removed from the mainland will have few species (hence, the light shading of island D). Islands B and C (medium shading) should have intermediary richness.

Metapopulation and metacommunity theory incorporates many of the same ideas about colonization and extinction in habitat patches, and so this theory also has appeal to some wetland researchers (Wissinger 1999; Semlitsch 2000; Cottenie et al. 2003; Kneitel and Miller 2003). A metapopulation is a set of small, spatially separated populations that are united together (Fig. 7.8). Even if an individual subpopulation becomes extinct, at least some of the subpopulations will survive, and colonists from the surviving patches will disperse back into extinct patches. Thus, a metapopulation persists in a balance of local extinction and colonization. A metacommunity simply consists of a set of metapopulations. In adapting metapopulation theory to management, Semlitsch (2000) maintains that for aquatic-breeding amphibians in wetlands, three crucial factors must be considered: (1) the number of individuals dispersing from individual wetlands; (2) the diversity of wetlands, especially in terms of hydroperiod; and (3) the probability of dispersal among adjacent wetlands or the recolonization of local populations.

Researchers have yet to test the whole of either island biogeography or metapopulation/metacommunity theory in wetland habitats. However, some portions of the theories

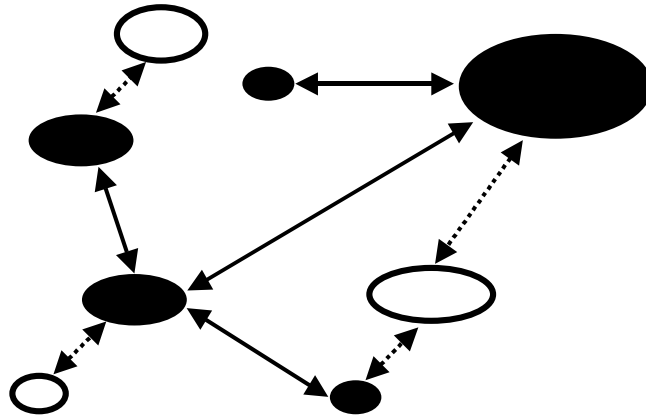


FIGURE 7.8

A metapopulation in isolated wetlands, with circles representing patches of wetland habitat. The filled circles indicate wetlands that are occupied by a species, and open circles represent temporarily vacant wetlands. Arrows indicate colonization pathways of the population. Theory suggests that vacant patches, where the population has gone extinct, will be eventually become recolonized by individuals from occupied patches.

have received attention, and below we review research on the importance of habitat isolation, habitat size, colonization, and extinction to wetland animal community development.

Habitat Isolation

Wilson, one of the original authors of the equilibrium theory of island biogeography, and Simberloff designed a direct test of the isolation aspect of the theory (Fig. 7.7) using wetland mangrove islands off the Florida coast. They first found all of the terrestrial animal species occurring on several small mangrove islands of varying distance from the mainland; this consisted of from 20 to 50 arboreal arthropods (spiders and insects) per island. Then they covered treatment islands with fumigation tents (the ones typically used for whole house pesticide treatments) and pumped in methyl bromide gas to kill all spiders and insects (only a few wood borers survived). Two control islands remained untreated. Recolonization of the defaunated wetland islands was then described. Simberloff and Wilson (1970) found that the islands nearest to the mainland were recolonized rapidly, and soon the species number reached an apparent equilibrium state (Fig. 7.9). The island farthest from the coast was colonized more slowly, and the equilibrium species number was lower than the other islands. The control islands maintained their normal species number, although community compositions varied over the study period. The results of this experiment supported the equilibrium theory of island biogeography in that equilibria seemed to develop and the equilibrium species number declined as habitats became more isolated from the source of colonists (Fig. 7.7). Natural disappearances also occurred on islands, even over the short study period, indicating that the extinction aspect of the theory was a frequent event.

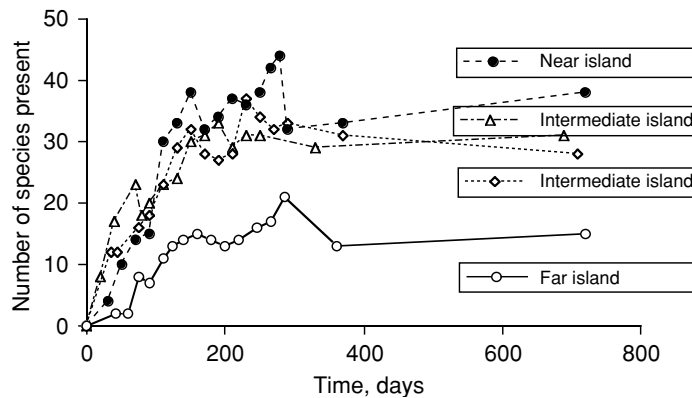


FIGURE 7.9

Postfumigation colonization curves for four small mangrove islands of varying proximities to the mainland sources of colonizers. Colonizers included an assortment of terrestrial insects and spiders. Proximity to the coast and community richness was related. The island nearest the coastline was colonized most rapidly, and the equilibrium species number was the greatest. The island farthest from the coast was colonized more slowly, and the equilibrium species number was lower. Figure was adapted from Simberloff and Wilson (1970) with the permission of the senior author and the Ecological Society of America.

For wetlands, habitat isolation can entail more than just a distance effect. Snodgrass and associates (1996) studied fish in isolated depressional wetlands of the southeastern United States. Despite lacking permanent surface connections to other water bodies and drying periodically, about 20% of the depressional wetlands supported fish. Apparently, these habitats can be colonized or recolonized by fish during periods of unusually high water. They found that fish occurred most frequently in depressional wetlands in close proximity to other aquatic habitats, but that proximity alone did not explain fish assemblage structure. The elevation difference between isolated wetlands and other water bodies was also important. If a significant elevation gradient existed between an isolated wetland and a nearby water body, fish movement was apparently inhibited. Snodgrass and associates (1996) maintained that connectivity, rather than simple proximity, was the factor most likely to influence movements of fish from source populations into isolated depressional wetlands. Baber and colleagues (2002) studied fish distributions in temporary wetlands of Florida, and they reiterated that the connectivity of isolated temporary wetlands with permanent water bodies played an importance role in community development. Gray and colleagues (2004) found that interwetland landscape complexity (mostly agricultural influences) can affect amphibian community composition in playa wetlands of the U.S. southern high plains.

As wetlands become increasingly isolated from each other due to habitat destruction and fragmentation, many animals populations will be threatened (Semlitsch 2000). A lack of certain species of amphibians (Lehtinen et al. 1999; Hamer et al. 2002), turtles

(Joyal et al. 2001), fish (Lafferty et al. 1999), and butterflies (Wettstein and Schmid 1999) has been associated with greater habitat isolation. However, wetland birds (Calme and Desrochers 2000), toads (Bradford et al. 2003), and insects (Brose 2003), which all have well-developed dispersal capabilities, were found to occupy even the most remote wetlands, indicating that not all wetland animal distributions are limited by habitat isolation.

Habitat Size

In ecology, it is generally accepted that a larger habitat will support more species than a smaller habitat (Fig. 7.7), given that other factors are equal. For example, wetland complexes that arise from beaver activity tend to include more types of habitats and subhabitats (open ponds, marshes, flooded forests, shrub swamps, abandoned wet meadows), and may contain more species than a comparably sized wetland of one type (Naiman et al. 1988). However, it is common for wetland researchers to find the relationship between animal species richness and wetland size to be rather weak, whether for birds (Calme and Desrochers 2000), amphibians (Kolozsvary and Swihart 1999; Snodgrass et al. 2000; Eason and Fauth 2001; but see Lehtinen and Galatowitsch 2001), or invertebrates (Schneider and Frost 1996; Wissinger et al. 1999a; Brose 2003; Batzer et al. 2004; Hall et al. 2004). However, for aquatic animals, both habitat size and water permanence may affect richness, and because size and permanence can be covariates (larger habitats are often more permanent; Wissinger et al. 1999a), isolating the influence of size will be complicated. Because the link between water permanence and species richness can be quite strong (Jeffries 1994; Schneider and Frost 1996; Kolozsvary and Swihart 1999; Wissinger et al. 1999a; Snodgrass et al. 2000; Eason and Fauth 2001; Batzer et al. 2004), some scientists have suggested that water permanence might be a useful replacement for habitat size when adapting island biogeography theory to wetlands (Ebert and Balko 1987; Brooks 2000). However, Hall and associates (2004) maintained that the ephemeral nature of many wetlands might preclude the development of an equilibrium between colonization and extinction, making it inappropriate to apply island biogeographic theory to temporary wetlands. Clearly, any attempt to associate faunal richness with wetland size must factor out the effects of permanence (and vice versa) before the analysis is clean. Muddying the waters further is the additional relationship between water permanence and predation (Fig. 7.5), which can either increase (by predator mediated coexistence) or decrease (by elimination of vulnerable species) taxa richness depending on interaction strengths.

The nature of wetland organisms might also contribute to a weak relationship between faunal richness and habitat size. A primary reason that habitat size is believed to affect diversity is that a larger habitat contains a wider range of microhabitats (Fig. 7.7), and this heterogeneity provides opportunities for a wider variety of organisms, especially specialists. However, wetlands are highly variable systems, and any specific set of microhabitat conditions might develop only sporadically. It would be risky for an animal to specialize on a narrow range of environmental conditions. Rather, being a generalist, capable of

coping with whatever conditions develop, might be the more prudent strategy (Batzer et al. 2004). Habitat generalists can probably persist in a variety of habitats, large and small, and thus habitat size becomes less important.

Because of the weak relationship between wetland size and faunal richness, and the fact that some wetland animals actually prefer small, ephemeral wetlands, Snodgrass and colleagues (2000) challenged the notion that discussions concerning wetland conservation or destruction should rely heavily on habitat size. Instead, they advocate focusing on conserving a diversity of wetland sizes and hydroperiods across landscapes.

Colonization of Wetlands

Many wetland animals are noted for their colonizing abilities. Insects and birds, the two most diverse animal groups in wetlands, probably achieve their dominance because flight enables them to find or escape from constantly changing wetland environments. When a previously dry wetland floods, insects and waterfowl arrive within days or even hours. Mosquitoes, midges, dragonflies, and beetles are often observed depositing eggs in wetlands as they become inundated (Streever et al. 1996; Brown et al. 1997; Mitsch et al. 1998; Wrubleski 1999; Keiper and Walton 2000). Waterfowl find newly flooded seasonal ponds to be especially valuable sites for foraging and nesting. However, despite the evidence for rapid colonization by many winged wetland taxa, few studies have actually quantified dispersal rates and gene flow for rapidly colonizing species (Bohonak and Jenkins 2004).

Sometimes, aerial colonization involves predictable, cyclic movements between habitats. It is well known that most wetlands birds migrate between habitats to breed and to overwinter. In addition, many insects migrate between permanent and temporary wetlands, and some possess a life history syndrome that involves wing dimorphism (Wissinger 1997; Langellotto and Denno 2001; see also Chapter 4). Long-winged adults of some beetles and water bugs overwinter in permanent habitats and then migrate to colonize re-filled temporary habitats in spring. Depending on the duration of the wet phase, one or more flightless short-winged, but highly fecund, generations are completed in those temporary habitats. As habitats dry, a dispersing generation of long-winged, but sexually immature, individuals develops that returns to permanent waters. This flight polymorphism not only facilitates dispersal but also allows for the rapid establishment of large populations in temporary habitats (Batzer and Wissinger 1996). Wing dimorphism is also prevalent in terrestrial planthoppers that inhabit coastal wetlands and research has revealed that (1) energetic trade-offs exist between reproduction and dispersal; (2) dispersal patterns are density dependent; (3) habitat heterogeneity helps maintain polymorphisms; and (4) life history strategies are affected by disturbance regimes (Denno and Roderick 1990, 1992; Langellotto and Denno 2001).

Even flightless wetland taxa arrive at newly inundated wetlands in remarkably short order. Petranka and associates (2003) found that seven amphibian species colonized some newly created wetlands during the initial wet cycle. Fish, which one would assume would have difficulty accessing isolated habitats, were found within a few years to have colonized

isolated beaver ponds created by damming seepage of closed peatlands (Ray et al. 2004). Despite being extirpated by periodic drought, fish (Snodgrass et al. 1996; Zimmer et al. 2000) and amphibians (Bradford et al. 2003) often are broadly distributed across complexes of isolated wetlands, indicating that habitat recolonization is rapid.

Small zooplankton and mites are assumed to disperse passively—either by wind, rain, or on animal vectors (Wiggins et al. 1980; Williams 1987). This assumption has been fostered by the widespread and cosmopolitan distributions of many zooplankton species, although Jenkins and Underwood (1998) note the scant evidence for zooplankton dispersal rates by wind or water. While there is considerable potential for internal and external bird and mammal transport of fish, amphibians, and invertebrates, and wind dispersal of resistant stages of small invertebrates, few studies have actually quantified colonization rates (Bilton et al. 2001; Okamura and Freeland 2002; Figuerola and Green 2002; Cáceres and Soluk 2002). One exception is for parasitic water mites that disperse while attached to their insect hosts (Bohonak et al. 2004). A second example is for fairy shrimp whose diapausing eggs can survive passage through the guts of salamanders that migrate to temporary wetlands to feed on these large, nutritious prey (Whiteman et al. 1996). Fairy shrimp dispersal rates estimated from genetic differences among populations are nearly identical to the colonization rates inferred from inter-habitat movements of salamanders (Bohonak and Whiteman 1996).

Three techniques have been used to quantify dispersal of wetland animals. The first is to use traps to estimate rates and distances of dispersal (e.g., Delettre and Morvan 2000). Lundkvist and colleagues (2002) used traps that mimic the reflectance spectra of wetland breeding habitats to estimate the movements of adult diving beetles and found that beetles that inhabit temporary waters were more mobile than those typically found in permanent wetlands. The use of stable isotopes is a second technique likely to become important for understanding animal dispersal (Hobson 1999). Caudill (2003) enriched natal habitats with a ^{15}N isotope and found that there was considerable movement of a mayfly among different ponds within a beaver wetland complex. Finally, dispersal rates can be inferred from estimates of gene flow (Bohonak and Roderick 2001). This technique relies on several critical assumptions (e.g., long-term equilibrium of drift and gene flow), and direct measurement of individual movements will always be an important benchmark for genetically inferred dispersal rates (Bohonak and Jenkins 2004). All of these methods will become increasingly important as ecologists pursue a landscape-level, meta-community (Fig. 7.8) understanding of ecological systems.

Many wetland animals that live in temporary wetlands (invertebrates, amphibians, fish) have desiccation-tolerant stages to complement other dispersal and colonization strategies (adaptations of animals for desiccation resistance are described in Chapter 4). One advantage of desiccation resistance is that it guarantees rapid establishment after refilling. Like plant seed banks, the “egg banks” of certain invertebrates can be long lived, and many species can deposit broods with individuals that hatch during different subsequent

wet-dry cycles (Adams 1984; Dodson 1987; De Stasio 1989; Taylor et al. 1990; Brendonck 1996; Cáceres 1997; Havel et al. 2000; Medland and Taylor 2001). The multiple generations that are stored in egg banks ensure that a diverse community of animals will be quickly established after drying events (Brock et al. 2003). The zooplankton community in refilling basins will not necessarily reflect the community composition before the previous drying event because of different dormancy periods and diapause strategies (Brock et al. 2003; Brendonck and De Meester 2003).

One strategy useful to assess the proportional contributions of persistence through desiccation resistance and recolonization is to compare the animals that emerge from experimentally rehydrated sediments with the communities observed when the basins refill (persistence + aerial colonization). Using this technique, Wissinger and Gallagher (1999) found that desiccation tolerance played a more important role in the reassembly of communities after an extended drought in temporary habitats (63–71% of all colonizers) than in an adjacent permanent wetland (38% of all colonizers). Similarly, Dietz-Brantley and associates (2002) found that aestivating invertebrates made up a significant component of colonization in Carolina bay wetlands. Anderson and Smith (2004) found that only 30% of all colonists in temporary playa wetlands of Texas originated from aestivating stages. The relative importance of desiccation tolerance may depend on the harshness of drying, and Anderson and colleagues (1999) predict that colonization from aestivating organisms should be least important in arid regions where substrates become inhospitable to most organisms.

Wetland invertebrates are excellent candidates for the study of dispersal, gene flow, and local adaptation for a variety of reasons including (1) the relatively discrete boundaries of wetland habitats; (2) the relative ease with which they can be sampled; (3) relatively large populations and short generation times that facilitate the estimation of population-level parameters; and (4) the frequent elimination, creation, or restoration of habitats by humans that offer opportunities to study colonization events.

Biogeographic Effects on Species Extinction

Animal extinctions, even at a local scale, are difficult to document because long-term study is typically required (see Semlitsch et al. 1996), and thus little empirical evidence on extinction events for wetland animals exists. Lafferty and colleagues (1999) used historical data on the distributions of the now endangered tidewater goby (*Eucyclobius newberryi*) from a series of isolated coastal wetlands in California to assess the relationship between habitat size and extinction. They found that, consistent with island biogeography theory, extirpation rates of this fish were greater in small than large wetlands and surmised that small wetlands were more sensitive to drought. For wetland fish, drought is frequently the mechanism for local extinction (Snodgrass et al. 1996; Baber et al. 2002). While invertebrates are also susceptible to drought, Jeffries (1994) found that invertebrate survival, even in drought-affected ponds, was ultimately dependent more on biotic processes such as predation or reproductive success than habitat drying. In Chapter 4, Mendelssohn and Batzer propose that most wetland animals

are well adapted to drought and for them, routine drying is not a significant constraint. Extinctions probably occur when an unusual condition develops in a wetland habitat, and not from natural environmental variation.

HABITAT HETEROGENEITY

Embedded in the concept that larger habitats will support more species is the idea that larger habitats will contain a broad range of subhabitats, offering opportunities for more species. Also, larger habitats are more likely to feature the natural processes, especially natural disturbances, which maintain a diversity of subhabitats and the species they contain.

Edge Effects

It has been long recognized that edges, or ecotones, the boundaries between habitats or subhabitats, are sites of increased species diversity because they tend to contain species that occupy each of the adjacent habitats as well as the actual edge (Leopold 1933; Yahner 1988). Wetland-upland boundaries would seem to be a particularly good example of this increased species diversity, especially in instances where the transition zone between the two habitats is large (Kilgo et al. 1998). Thus, a target of management prescriptions by early wildlife biologists often included a mosaic of juxtaposed habitats with an optimal amount of edge (Leopold 1933).

More recently, it has been recognized that there are also negative effects associated with certain types of edge (Gates and Gysel 1978; Paton 1994). For example, bird nests can have decreased survival in smaller forest fragments (Wilcove 1985) or in landscapes with more fragmentation of forest habitats (Robinson et al. 1995). The cause is generally believed to be increased numbers of and/or vulnerability to a variety of nest predators attracted to edge situations. In some landscapes, increased fragmentation also makes remaining fragments more vulnerable to brood parasites such as the Brown-headed Cowbird (*Molothrus ater*) (Robinson et al. 1995). Also, increased desiccation that can occur along the edges of forests has been shown to decrease the abundance of litter-dwelling arthropods (Burke and Nol 1998).

However, the notion of decreased productivity along forest habitat–open habitat edges does not necessarily hold for all habitats or taxa. For example, juxtaposition of wetlands with certain types of uplands appears to be a necessary feature in the life history of many species of aquatic herpetofauna (Gibbons 2003). Many species of forest-dwelling amphibians require nearby wetlands for breeding (Semlitsch 1998, 2000). Conversely, some aquatic organisms such as turtles require a safe adjacent upland habitat in which to lay their eggs or to hibernate (Buhlmann 1995; Burke and Gibbons 1995). In some cases, wetland-upland boundaries may be travel routes for predators, but this is poorly documented. And it is likely that watercourses can serve as pathways for some predators and brood parasites to access otherwise intact forests, but evidence is again lacking.

Evidence of negative effects of edges on avian nest success in wetland ecosystems, mainly bottomland hardwood forests, is equivocal. Saracco and Collazo (1999) found approximately 90% of artificial nests placed near ecotones between bottomland forest and agriculture were depredated, compared with about 55% along forest-river edges. Moorman and associates (2002) reported that Hooded Warbler (*Wilsonia citrina*) nest success was unaffected by distance to edge in a bottomland forest, but that likelihood of nest parasitism was greater near clearcut edge. Twedt and colleagues (2001) found that timber harvest negatively affected nest success in tree-nesting birds in bottomland forests. However, nest success of a variety of bottomland forest songbird species was unaffected by creation of openings in a companion study. Nest success in that study was more likely related to flooding patterns, which provide protection for nests and may affect predator behavior (Wood 1999). Also, edge effects at the local scale are likely to be mediated by factors operating at larger spatial scales, such as degree of fragmentation in a landscape; thus, edge effects on nest success are variable (Rodewald 2002).

Gap Dynamics

Habitat heterogeneity in general and edges in particular are created by natural disturbances such as fire, floods, extreme weather events, and insect outbreaks, and by human activities such as agriculture, logging, and urbanization. On a smaller scale, in forested wetlands, gap-phase dynamics is an ongoing natural process. In general, these processes maintain a diversity of subhabitats within an overall habitat type or ecosystem (e.g., a variety of successional stages and species dominance patterns within a bottomland hardwood forest), and are key processes for maintaining biodiversity in the system. However, disturbances have a spatial and temporal scale, and effects on a system or level will depend on those scales (Pickett et al. 1989).

In forested wetlands, canopy disturbance is a major factor affecting forest structure and composition, and can in turn affect animal community structure (Moorman and Guynn 2001). Tree-fall gaps represent a distinct microhabitat that differs from the understory of the surrounding forest in vegetation structure, plant species composition, and microclimatic conditions. If gaps are large enough, species associated with early successional habitats will occupy them (Moorman and Guynn 2001). Arthropods, in particular, seem to respond positively to gaps (Blake and Hoppes 1986), although more work is needed on this topic, especially in bottomland forests. For example, insect abundance and distribution were influenced by flooding as well as by canopy disturbance in an Arkansas bottomland forest (Gorham et al. 2002). Blake and Hoppes (1986) captured more birds in gaps compared with the adjacent forest understory in an upland woodlot. Kilgo and associates (1999) captured more birds during fall migration in the largest (40-m radius) artificial gaps than in gaps of smaller size in a bottomland forest. Using the same study sites, Menzel and colleagues (2002) found more bat activity in forest gaps and Carolina bay wetlands than in forested habitats, probably because these habitats provided an open area in which to forage. However, several researchers have found decreased abundance

of salamanders in bottomland forest gaps (Cromer et al. 2002) or in clearcuts (Clawson et al. 1997; Perison et al. 1997) compared with the forest interior. Differences were likely due in part to increased temperatures in forest openings, but clearcuts also contained less litter, an important habitat component for salamanders.

Hemi-marsh Concept

The realization that freshwater marsh habitats that contained a roughly equal mixture of open water and emergent plant cover (or hemi-marsh) are most productive for waterfowl has long been a tenet for managing marshes for wildlife (Weller 1978). Whether caused by natural succession (Fig. 7.6; Murkin et al. 2000), fire (De Szalay and Resh 1997), or mechanical mowing (Murkin et al. 1982; Batzer and Resh 1991; De Szalay and Resh 1997), waterfowl and invertebrate use of marshes tends to peak under heterogenous hemi-marsh conditions. Numerous ecological mechanisms probably contribute to this response. Hemi-marshes typically develop soon after drought events or other disturbances and are thus in the early regenerating stage of succession (Fig. 7.6). Assorted foods for animals are present, including seeds from annual plants, detritus, algae, and invertebrates. The interspersed plant stands provide substrates for invertebrates, nesting sites for birds, and protective cover from predation for many animals. Open water patches provide habitat for fish and foraging waterfowl (Murkin and Caldwell 2000) and are attractive to aerially colonizing insects (Batzer and Resh 1991; De Szalay and Resh 1997). The edge habitat between plant and open water patches may provide additional animal habitat (Murkin et al. 1992)

FOCAL WETLAND ANIMALS

While all animal species will contribute to the functioning of wetland ecosystems, some play particularly crucial roles. Names attributed to these species include “keystone species” or “ecosystem engineers.” Each has a significant impact on numerous other species in a system through predation, buttressing food webs, or physically modifying habitat structure. Some other species may not play such crucial roles in wetland ecosystems but are sensitive to ecological changes and may serve as indicators or bellwethers of environmental impacts. Next, we discuss the ecology of what we consider some of the most important animal species or groups in wetlands, acknowledging that numerous deserving animals do not appear in our list.

BEAVERS

The beaver is a large rodent indigenous to much of North America (*C. canadensis*) and parts of Europe and Asia (*C. fiber*). Beavers play a unique role in wetland ecology because, other than man, they are the only organisms capable of creating wetlands (Muller-Schwarze and Sun 2003). The beaver is often cited as the archetypical example of an ecosystem engineer. Jones and associates (1994) defined *ecosystem engineers* as organisms that directly

or indirectly modulate the availability of resources to other species by causing physical state changes in biotic or abiotic materials. The ecological importance of the beaver stems largely from habitat modifications resulting from their dam-building activities.

The construction of a beaver dam initiates a sequence of events (Naiman et al. 1988; Hammerson 1994). The area behind the dam becomes flooded, and a channel or smaller wetland area is converted into a pond. Any upland trees or shrubs in the pond area die as soils around their roots become anoxic. Shoreline forests are also modified because beavers cut riparian trees or shrubs for food and building material. With the loss of trees, the pond canopy opens. The open water pond is then invaded by aquatic plants (pond weeds, lily pads). This "beaver pond" condition can persist for many years. Eventually, however, the beaver colony will die out from disease, or the colony will move from the area as food resources become limited. After abandonment, the dam will erode and breach, and the pond will drain. The plant seed bank in the exposed sediments will sprout, and a wet meadow habitat will develop. Slowly, trees and shrubs will reinvade, and the habitat will eventually revert back to its former forested state.

During this sequence, an assortment of important hydrologic, biogeochemical, and ecological processes are affected (Naiman et al. 1988; Naiman et al. 1994). After dam construction, the overall precipitation storage capacity of the habitat will increase due to the pond, and the variability in discharge and the current velocity of the stream will decline. The water table in the affected area may become elevated. Sediments being carried downstream will settle in the pond, and downstream turbidity may decrease. Oxygen dynamics will change, and hypoxic or anoxic conditions may develop in the pond area as plants killed by flooding decay. As mentioned earlier, a formerly upland plant community will be replaced by a wetland flora. In addition, planktonic algae may become more prevalent in the wetland pond than they were in the precursor stream channel. The stream invertebrate community will be replaced by a wetland fauna, and the functional nature (see Table 7.2) of this community will change. A community previously dominated by collector-filterers that filter food from flowing water and scrapers that graze on rock surfaces will be replaced by a community dominated by collector-gatherers that gather particles from surfaces and by invertebrate predators. Rolauffs and colleagues (2001) found that the dam itself supports a unique invertebrate fauna. Although the original stream channels generally support many more aquatic invertebrates than a wetland pond on a per m² basis, the much larger wetted area of the beaver pond will produce a greater total biomass of these animals. A stream herpetofauna dominated by salamanders and snakes may be replaced by a pond fauna dominated by frogs, turtles, and lizards (Metts et al. 2001). Flow-dependent lotic fishes will be replaced by lentic fishes, and early colonizing small-bodied fish will be replaced by larger-bodied predators as the ponds age (Snodgrass and Meffe 1998; Collen and Gibson 2001). Even after the dam is abandoned and the pond drains, there is a characteristic fish fauna associated with heavily vegetated channels that flow through wet meadows (Snodgrass and Meffe 1998). Finally, an assortment of birds, particularly waterfowl, find beaver ponds to be prime foraging, roosting, and brood-rearing sites (McCall et al. 1994).

The recovery of the beaver from the severe population depression that occurred during the fur-trapping era has had important consequences for landscape ecology (Muller-Schwarze and Sun 2003). Naiman and associates (1994) reported that 13% of the land in a 300 km² area of northern Minnesota was converted into new beaver meadows and ponds from 1927 to 1988. However, over a similar period in South Carolina, Snodgrass (1997) reported only 0.5% of the overall landscape was influenced by beavers. Beaver-created habitats can significantly alter the patch dynamics of landscapes (Wright et al. 2004), although the importance of beavers may vary regionally.

MUSKRATS

The muskrat is another aquatic rodent found throughout North America, and in much of Europe and Asia where it has been introduced by man. Fully grown, they measure about 60 centimeters in length and weigh about 1.5 kilograms. Muskrats are chiefly herbivores, eating various wetland plants, especially cattails (*Typha*) and bulrushes (*Scirpus*) (Clark 2000); they also use the leaves and stems to construct houses. Because their herbivorous behavior can affect wetland succession, the muskrat, like the beaver, has been touted as an ecosystem engineer.

In a classic book on muskrat population ecology, Errington (1963) describes how muskrat numbers undergo cyclic population fluctuations induced by social and physiological factors interacting with predation and disease. Errington suggested that when muskrat populations become high, they can decimate stands of emergent wetland plants in events called *eat-outs*. In fact, muskrats have long been considered a primary factor in the development of "lake marsh" conditions (Fig. 7.5), and this role in marsh succession contributes to the ecosystem engineer moniker. However, Clark (2000) maintains that little empirical evidence exists to demonstrate that muskrat herbivory can eliminate stands of cattails or reeds. In a study at Delta Marsh, Canada, he estimated how much of the total standing crop of emergent vegetation was removed by muskrats through cutting, consumption, and wastage. He found that at most 11% and as little as 1% of the plant standing biomass was removed by muskrats, even where populations were high. Clark concluded that muskrats may contribute to declines of emergent vegetation but suggests that the term *eat-out* overstates their importance. He further notes that where *eat-outs* have been reported, the events often coincide with high water events and speculated that declines of emergent vegetation might have been mostly related to undesirable hydrologic conditions for the plants. Muskrats in general do poorly when water fluctuations are extreme (Virgl and Messier 1996), perhaps because their food supply is inhibited.

Even if muskrats are not ecosystem engineers, they are still very important to marsh ecology. Connors and associates (2000) found that muskrat activity (feeding, burrowing, house formation) increased nitrogen mineralization and nitrification rates, and thus influenced wetland soil nitrogen dynamics. They anticipated that muskrats would increase floristic diversity by thinning monoculture stands of cattail, but their study did not

support that hypothesis. De Szalay and Cassidy (2001) found that the open water halo surrounding muskrat lodges supported an invertebrate community that was different from the community in intact plant stands. An important role of muskrats may be in creating more spatially complex stands of emergent plants, providing opportunities for a greater variety of animals. Muskrats may also influence litter decomposition. Freshly cut plant material has different nutritional qualities than postsenescent detritus (van der Valk and Davis 1978b), and cut material is generally concentrated around muskrat houses; both factors produce unique conditions for decomposition (Clark 2000). Besides creating the hemi-marsh conditions that waterfowl prefer (see earlier), the houses that muskrats build are commonly used as waterfowl nesting platforms. Not all ecological impacts of muskrats are positive. In Eurasia, where the muskrat is an exotic invader, they may alter the structure of indigenous plant communities (Smirnov and Tretyakov 1998).

COLONIAL WADING BIRDS

Of all bird orders, arguably the one with the greatest percentage of species adapted to wetland habitats is the Ciconiiformes, or wading birds (Sprunt et al. 1978). The order consists of the herons, egrets, and bitterns (Family Ardeidae); ibises and spoonbills (Family Threskiornithidae); storks (Family Ciconiidae); and flamingoes (Family Phoenicopteridae). Other than spoonbills and flamingoes, whose bills are adapted for filter feeding in shallow water, wading birds are well adapted to feed in both terrestrial and shallow water habitats. Their legs are long and unfeathered, with long, unwebbed toes that provide a solid footing in a variety of substrates. Their bills are long and pointed, allowing them to feed on a variety of prey, from fish, crabs, and other aquatic prey to small mammals and large insects in pastures. For the most part, though, wading birds, as the name implies, are tied to water in some way.

Of the various ways that wading birds are tied to water and wetlands, perhaps none is more intriguing, or has been the subject of more theoretical discussions in the literature, than their propensity for forming breeding colonies. Also known as *heronries* or *rookeries*, wading bird colonies can vary in size from a few breeding pairs of a single species to thousands of pairs of multiple species. Nests are usually placed in small trees or shrubs, often with many nests per tree. Colony sites are often traditional, in that they are used year after year, although they tend to slowly migrate as nesting substrate is gradually lost in portions of the colony. Thus, between the increased number of large birds in a particular area, and the fixed location of the colony over time, the colony site is both conspicuous to potential predators and is likely to result in a depletion of prey in the immediate area around the colony. What, then, is the advantage for these birds to nesting colonially?

First, although the colony site is conspicuous to predators, it often has several features that make it resistant to widespread nest predation. The exact colony location is critical. Often, the colony is located on an island surrounded by deep water, thus discouraging many terrestrial mammalian predators. In the southeastern United States, the presence of alligators enhances protection against significant nest predators such as raccoons (*Procyon lotor*). The

alligators benefit from the occasional nestling that loses its balance and falls into the water, but the advantage to the birds far outweighs these losses. With many nesting pairs, there are also many eyes to watch for predators, thus discouraging other predators such as crows.

Second, although food can become locally depleted near the colony, the colony can actually serve as a means of transferring information about food location. According to the information center hypothesis, birds in the colony can learn about location of food from birds arriving at the colony with food (Ward and Zahavi 1973). Information transfer would be especially important for species that feed on clumped prey that are locally abundant, such as fish schools, but are unpredictable in space and time. For example, Great Blue Herons (*Ardea herodias*) breeding in colonies were most likely to depart in the direction from which successfully foraging individuals returned to the colony with food (Krebs 1974). Because wading birds often forage in groups as well, the departing bird is more likely to find an exact location where it can successfully capture its patchily distributed prey.

Another important consequence of many large birds nesting in one location is the local increase in nutrient availability. Studies conducted at communal roosting and nesting assemblages indicate substantially enhanced local nutrient availability as the result of the deposition of excreta (Hutchinson 1950; Onuf et al. 1977; Oliver and Legovic 1988). In addition, Bildstein and colleagues (1992) found that the mass of nutrients imported to a South Carolina estuary by White Ibis (*Eudocimus albus*) from nearby freshwater feeding sites was substantial when compared with those from atmospheric sources and could vary considerably among years.

Because of the importance of conserving wading bird colony sites, many fish and wildlife agencies maintain a wading bird rookery atlas, which includes the species composition and location of the rookeries. In addition, a North American Waterbird Conservation Plan, a continent-wide conservation plan for wading birds and other colonial waterbirds, has been developed (Kushlan et al. 2002). The focuses of this plan include determining the status of waterbird populations, monitoring population numbers and demographics, identifying key factors in maintaining waterbird populations, and identifying and conserving important bird areas such as rookery sites. Other specific issues involving wading birds include contaminants and damage to aquaculture facilities by fish-eating species (Kushlan and Hafner 2000). As with other large-scale conservation efforts, the success of colonial waterbird conservation will depend on an ecosystem approach to management with the participation of many partners.

ENVIRONMENTALLY SENSITIVE BIRDS

The term *environmental indicator* can have several meanings. For example, an organism can be an indicator of the negative effects of some sort of perturbation, such as a pollutant. Or, an organism can be so closely associated with a particular habitat that, should that habitat be reduced in size or otherwise perturbed severely enough, that organism can be measured and can serve as a metric of the degree of perturbation of that system.

Birds have been and continue to be important indicators of both kinds of perturbations (Furness and Greenwood 1993; Kushlan 1993; Novak et al. in press). A classic example of an indicator of a pollutant otherwise unseen is the response of upper trophic level birds to organochlorine insecticides such as DDT (dichloro-diphenyl-trichloromethane). These highly persistent pesticides, used for control of mosquitoes and other insect pests, tend to magnify in concentrations at higher trophic levels. In addition to immediate mortality in high doses, fish-eating birds such as herons and egrets, Brown Pelicans (*Pelecanus occidentalis*), Ospreys (*Pandion haliaetus*), and Bald Eagles (*Haliaeetus leucocephalus*), and other raptors such as Peregrine Falcons (*Falco peregrinus*), which feed on shorebirds and waterfowl, exhibited thinning of their eggshells to the point where the eggs were crushed during incubation. Not surprisingly, each of the above species was federally listed as threatened or endangered at some point. Since the restriction of the use of DDT in the United States in the 1960s and 1970s, raptor populations have rebounded.

Similarly, waterbirds can serve as monitors of a variety of other pollutants, including heavy metals, radionuclides, acidification, oil, and air pollution (Furness and Greenwood 1993). For example, waterbirds exhibited massive reproductive failures in response to elevated levels of contaminants, especially selenium, in agricultural wastewater ponds and the Kesterson Reservoir in the San Joaquin Valley, California (Ohlendorf et al. 1989). When unhatched eggs of species such as American Avocets (*Recurvirostra americana*) and Black-necked Stilts (*Himantopus mexicanus*) were investigated, the embryos frequently exhibited bizarre deformities caused by elevated selenium levels. Again, as higher trophic level organisms, waterbirds contained magnified levels of contaminants that could have otherwise gone undetected.

In addition to being indicators of the negative effects of pollutants, birds are sometimes so intimately tied to a particular habitat type or ecosystem that they can therefore serve as an indicator of the integrity of that system. By integrity, we mean a system that contains all of its native biodiversity and the ecological processes that maintain that biodiversity. For example, throughout most of the United States, Clapper Rails (*Rallus longirostris*) are found only in salt and brackish marshes and mangroves (Eddleman and Conway 1998). Therefore, if these habitats decline in quality or quantity, we would expect to see a negative response by Clapper Rails, as noted by Novak and associates (in press). They found decreased eggshell integrity and increased DNA strand breakage in populations exposed to polychlorinated biphenyls and metals.

In fact, virtually every major ecosystem type has at least one bird species that is closely associated with that ecosystem, and therefore, those species should serve as effective indicators of the health of their respective ecosystems. For example, Ormerod and Tyler (1993 and citations therein) described the relationship between aspects of Dipper (*Cinclus cinclus*) breeding ecology and stream quality. Similarly, the Louisiana Waterthrush (*Seiurus motacilla*) can serve the same function in streams of the eastern United States (Brooks et al. 1998). Although aquatic invertebrates are the most widely used indicators of stream water quality, they may not reflect conditions within larger scales. For

example, landscape scale perturbations that fragment forests may have no effect on water quality but can lead to increased nest predation and parasitism levels. It is likely that bioindicators that combine birds and invertebrates will be superior to either alone (Brown and Batzer 2001).

In forested wetlands, the Prothonotary Warbler (*Protonotaria citrea*), a cavity-nesting songbird of the southeastern United States, has been shown to be sensitive to certain perturbations that affect ecosystem integrity (Wood 1999). Nest success was not affected by timber harvests that removed trees in patterns designed to mimic natural disturbances such as wind or ice storms or prolonged flooding. However, nest success was related to interannual variation in hydrology. In years when plots were partially flooded, water provided some protection from nest predators to nests built over inundated areas. Dry years, or years of prolonged flooding, had decreased nest success. This same relationship was found experimentally by Hoover (2003). Similarly, productivity by Wood Ducks (*Aix sponsa*) in South Carolina bottomland forests was related to wetland hydrologic conditions (Kenamer 2001). Thus, perturbations that affect the natural hydrology of large river floodplains are likely to be manifested in decreased productivity of these species.

Although there are many other examples of birds as potentially effective indicators of wetland ecosystem integrity, exact metrics have not been developed for the most part. For example, potentially appropriate metrics of integrity might include the following characteristics of colonial waterbird populations: genotoxicity, mixed function oxidases, metallothionein induction, tissue concentration of contaminants, eggshell quality, other physiological responses, histopathology and teratology, growth, behavior, reproductive performance, mortality, presence/absence, distribution, and population indices (Kushlan 1993). If a population fails to show an effect using one metric, does it mean that there is no effect, or that the wrong metric was used? Clearly, use of several metrics (and indicator species) is desirable, and development of useful metrics relating avian indicator species to their ecosystems would seem to continue to be a fruitful area of research.

WETLAND FISH

After hydrology, some argue that the presence or absence of fish is the most important factor influencing the ecology of aquatic animal communities in wetlands (Wellborn et al. 1996; Zimmer et al. 2002; Fig. 7.5). Fish are top-predators in many wetlands, and thus when present, they can dramatically affect the structure of lower trophic levels. When many people think about fish in wetlands, large individuals come to mind. However, while several large-bodied species inhabit wetlands, in terms of ecological function, it is probably small individuals (larval forms or diminutive species) that are most important. In salt marshes, large fish are mostly restricted to tidal creek channels, while the bulk of a salt marsh expanse is dominated by small species such as *Fundulus* (Kneib 1997b; West and Zedler 2000), gobies (Laffaille et al. 2000; Thomas and Connolly 2001), or assorted immatures (Mathieson et al. 2000; Thomas and Connolly 2001). In tidal freshwater

systems, a similar pattern develops (Castellanos and Rozas 2001). In isolated depressional wetlands that support fish (many are fishless), the fish community is dominated by small species such as small sunfishes, small minnows, sticklebacks, mosquitofish, or topminnows (Snodgrass et al. 1996; Zimmer et al. 2002). Even in river floodplains, where large fish are commonly observed, empirical sampling indicates that most fish in floodplains are small (Ross and Baker 1983; Lewis et al. 2001).

Despite their size, these small fish can exert a significant influence on wetland ecology. A small wetland fish species that has been demonstrated to be very important ecologically is the fathead minnow (*Pimephales promelas*). Fatheads are widely distributed in prairie wetlands across north central North America. Zimmer and colleagues (2002) found that fathead minnows had numerous ecosystem impacts on prairie wetlands, including suppressing salamander and invertebrate numbers and increasing algal chlorophyll *a* concentrations, presumably via a trophic cascade from planktivore reductions (Fig. 7.4). Zimmer and colleagues (2000) and Tangen and associates (2003) found that the presence or absence of fathead minnows had more influence on the invertebrate community structure in prairie wetlands than did water chemistry, peripheral agricultural practices, or past drainage history.

To assess predatory impacts of fish in some New York marshes (Batzer 1998; Batzer et al. 2000), enclosure/exclosure experiments were used to manipulate densities of adult and larval fish (carp and brown bullheads). Although the large adult fish did not have a detectable impact on small fish or invertebrates, larval fish had a dramatic impact on densities of bottom dwelling midges (Batzer 1998). The impacts of fish on invertebrate prey living in beds of submersed pondweeds were less obvious, however. While mud substrates supported midges almost exclusively, a wide assortment of invertebrates inhabited plant surfaces, including numerous predatory forms (damselflies, water bugs). Batzer and associates (2000) found that although fish were clearly consuming midges, experimental exclusion of fish unexpectedly harmed rather than benefited the midges. They concluded that fish were also consuming invertebrates that were predators and competitors of midges, and these indirect beneficial effects of fish on midges were more than compensating for any negative direct effects. Because most wetland fish are omnivorous (feed on more than one trophic level), assessing their impacts on food webs can be complex (Fig. 7.4).

The importance of indirect effects of fish predation has been more thoroughly examined in salt marshes with the killifish *Fundulus heteroclitus*. Kneib and Stiven (1982) manipulated densities and size classes (small, medium, and large) of *F. heteroclitus* in large marsh enclosures and found that small surface dwelling invertebrates were suppressed by small fish, but were enhanced by larger fish (>7 cm). They hypothesized that small fish fed directly on the small invertebrates, but larger fish were instead consuming a secondary predator, the grass shrimp (*Palaemonetes pugio*). The suppression of grass shrimp densities indirectly benefited surface dwelling invertebrates. Subsequent work by Posey and Hines (1991) further suggested that top-down control of grass shrimp by *F. heteroclitus* has a range of effects because the grass shrimp also fed on predatory anemones, and thus

responses of basal species in the food webs were variable. When predatory fish are common in wetlands, they probably have important impacts on food web dynamics, but the end result of impacts may at times be difficult to predict without careful experimentation.

While we have focused on the impacts of small fish, large fish should not be overlooked. Besides being the source of larval progeny, an important ecological influence of large bodied fish is through bioperturbation. The common carp (*Cyprinus carpio*) is a large Eurasian minnow that is now established in wetlands throughout the world. The bottom-feeding behavior of large adult carp is believed to affect water-column and benthic ecological processes. Several studies have tested that hypothesis by manipulating adult carp densities or biomass, and these studies suggest that carp activity increases water turbidity (King et al. 1997; Loughheed et al. 1998; Angeler et al. 2002; Schrage and Downing 2004), total phosphorous and nitrogen levels (Angeler et al. 2002), and sediment oxygen demand and particle settlement rates (Robertson et al. 1997). Combined with their trophic impacts on invertebrates (Batzer 1998; Loughheed et al. 2004; Schrage and Downing 2004) and indirectly on phytoplankton, carp may be keystone organisms in many wetlands.

AMERICAN ALLIGATORS

The American alligator (*Alligator mississippiensis*) is a large crocodylian endemic to the southeastern United States from eastern North Carolina to eastern Texas. Adults typically reach a length of 4.0 to 4.5 meters but have been reported as long as 6 meters, weighing in excess of 1000 pounds. They primarily inhabit freshwater swamps and marshes but are also associated with rivers, lakes, and smaller bodies of water. They are a classic example of a keystone species, partly because they are apex predators in most of the systems they inhabit, but mainly because their behavior includes creation of deeper open water areas, or alligator holes, that retain water when the marsh or floodplain is dry (Meffe and Carroll 1997). Holes are often connected via one or a series of tunnels or dens, which they also excavate (McIlhenny 1935).

Alligators have a reciprocal relationship with wetlands—they depend on them, but some wetlands, especially the southern Florida Everglades, are shaped by them in return. Alligators use their mouths, tail, and webbed hind feet to dig and thrash out a small hole about the size of their body, which is gradually enlarged. The material thrown out around the holes forms a raised berm high enough to support trees and other woody vegetation in an otherwise treeless environment. The trees support a number of biota that would not otherwise be present. Similarly, cattails, arrowleaf, and other emergent vegetation grow around the margins of the hole, and floating leaved plants become established in the open water. Holes can take on different structures and contain different plant species depending on surrounding vegetation (Palmer and Mazzotti 2004). Alligator holes thus increase spatial heterogeneity, influence plant community composition and structure, and increase biological diversity.

The area of open water is kept free of thick mats of plants by the activity of the alligators. Many small aquatic organisms, such as grass shrimp, water fleas, and mosquitofish,

spend their lives within a single alligator hole. The holes also aggregate populations of fish and shellfish, turtles, and other herpetofauna, attracting other predators such as raccoons, mink, and wading birds.

Alligators also build their nests on raised areas such as stream banks so as to keep them out of the water during times of flooding. These nest mounds, which are made from sticks, leaves, small branches, and mud, provide relatively dry refugia for terrestrial animals during such times. Several turtle species, especially the Florida red-bellied turtle (*Chrysemys nelsoni*), routinely use the base of alligator nests to deposit and incubate their own eggs (Goodwin and Marion 1977; Deitz and Jackson 1979). Over time, the nests also decompose to form peat. Peat fires, long in duration but cooler and slower moving than catastrophic wildfires, are common in the Everglades and are an important process in that ecosystem.

The importance of alligator holes as sites of concentrated biological activity becomes critical during dry seasons. The hole itself retains water and is a place where the alligator can wait out the dry period until the winter rains. During droughts, the holes are refugia for many aquatic organisms, offering resilience for populations over broad spatial scales. Alligator holes become critical foraging sites for wading birds such as herons and egrets, which would likely be unable to find adequate food in the marsh otherwise. Until the 1960s, the Everglades provided the primary nesting area for wading bird populations in the southeastern United States. Since then, only 5% to 10% of the populations that once nested there continue to use the area (Ogden 1978, 1994), likely due to alterations to hydrology (i.e., less wet season habitat) caused by development. Thus, alligator holes are likely to become even more critical for wading birds and other wetland biota on a year-round basis, justifying the claim that the alligator is the keeper of the Everglades.

AMPHIBIANS

Wetland amphibians consist of two main groups: (1) frogs and toads (or anurans) and (2) salamanders. Both groups rely on wetlands for reproduction. On maturation, some amphibian adults (bullfrogs, sirens) remain in wetlands, while others (ambystomatid salamanders, treefrogs) live terrestrially, only returning to the wetlands to breed. A small number of salamanders exhibit flexible life histories in which larvae either metamorphose into terrestrial, "metamorphic" adults or retain a larval morphology and remain aquatic as "paedomorphic" adults (Whiteman 1994).

Most anuran larvae consume algae or detritus, and competition for these resources can develop (Werner 1992). Some anuran larvae will prey on small invertebrates or eggs and larvae of other amphibians, suggesting that functional roles of anuran larvae in food webs may be complex (Petranka and Kennedy 1999). Despite the belief that many tadpoles are important primary consumers, the degree to which they affect detrital breakdown or algal standing stocks and productivity in wetlands is largely unknown.

Salamander larvae are carnivorous and have multiple trophic roles in wetland food webs including (1) reciprocal predator-prey interactions with large invertebrate predators such as

dytiscid beetles and dragonfly nymphs (i.e., they prey on and are preyed on by these invertebrates; Morin 1981, 1983a; Wissinger et al. 1999a; Yurewicz 2004); (2) competition with invertebrate predators for shared prey (Caldwell et al. 1980; Wilbur and Fauth 1990); and (3) when there are more than one species, interacting simultaneously as competitors, intraguild predators, and cannibals (Morin 1983b; Yurewicz 2004; Whiteman and Wissinger 2004). In some cases, salamander larvae increase invertebrate and/or anuran diversity via predator-mediated coexistence (e.g., Morin et al. 1983; Fauth 1999), whereas elsewhere they eliminate vulnerable prey species (e.g., Morin 1983a; Wissinger et al. 1999b). In fishless permanent wetlands with paedomorphs, salamander populations may contain many different cohorts, and smaller conspecifics may be cannibalized (Whiteman and Wissinger 2004). Although salamanders may be the top aquatic predators in many temporary wetlands, few studies consider their potential to exert top-down control on food webs (Blaustein et al. 1996).

Hydroperiod (degree of water permanence) variation influences amphibian distribution, and the presence or absence of fish, often a covariate of hydroperiod, is perhaps the most important determinant of amphibian community composition in wetlands (Skelly et al. 1999). Within a genus, different anuran species can replace each other along permanence gradients, and the predator-permanence model of Wellborn and associates (1996), discussed earlier (Fig. 7.5), was in part developed to explain these replacements. Several evolutionary/ecological trade-offs underlie replacements. One trade-off is between the high activity and growth rates that facilitate timely metamorphosis in temporary habitats and the relatively low activity, risk-sensitive foraging behaviors that facilitate coexistence with predators (salamanders in long-duration temporary habitats and fish in permanent habitats). Such trade-offs may explain the replacement of chorus frogs (*Pseudacris triseriata*) or *Hyla gratiosa* treefrogs in vernal wetlands by spring peepers (*Triseriata crucifer*) or *Hyla cinerea* treefrogs in permanent or semipermanent habitats with salamander or fish predators (Skelly 1995, 1997; Leips et al. 2000). A second trade-off involves predator-avoidance strategies. For example, green frog larvae (*Rana clamitans*) are better at avoiding dragonfly predators than bullfrog larvae in temporary habitats, but the reverse is true for the avoidance of fish predators in permanent ponds (bullfrog larvae are unpalatable to fish; Werner and McPeck 1994; Peacor and Werner 1997; Eklov 2000). Many anuran larvae exhibit phenotypic plasticity in behaviors, morphology, and physiology, depending on the density and types of predators and competitors present (McCollum and Van Buskirk 1996; McCollum and Leimberger 1997; Van Buskirk 2000; Relyea and Werner 2000; Relyea 2001). This plasticity is common in wetlands where inter-annual variation in hydroperiod creates temporal variability in the presence or absence of predators and competitors.

The worldwide decline and disappearance of amphibians has focused attention on these animals and led to a flurry of experimental research and monitoring of amphibian distribution and abundance (Pechmann et al. 1991; Alford and Richards 1999; Houlahan et al. 2000; Alford et al. 2001; Collins and Storfer 2003). A number of conservation issues associated with the amphibian decline focus on wetland species. Despite government protections, wetlands—especially small, isolated, temporary habitats—continue to

decline. Many amphibians breeding in these habitats can not maintain viable populations in permanent habitats with fish. Indeed, conservation of amphibian biodiversity is one of the strongest and best-documented reasons for protecting small, isolated wetlands (Semlitsch and Bodie 1998; Semlitsch 2000). A second issue is related to the rapid increase in constructed wetlands to mitigate for encroachment on small natural wetlands. The most important flaw in the design of constructed wetlands is that they are too deep and too permanent compared with the natural wetlands they are designed to replace (Mitsch and Wilson 1996). Because of the strong negative effects of fish predators (and aggressive permanent-habitat amphibians such as bullfrogs), pond-like mitigation wetlands will have different species compositions than the destroyed natural habitats (Adams 2000; Snodgrass et al. 2000). Ambystomatid salamanders should be particularly vulnerable to details of hydroperiod in mitigation wetlands—fish are likely to be present if they are too permanent, and there will be insufficient time for larval development if they are too ephemeral (Semlitsch 1987; Kats et al. 1988; Rowe and Dunson 1995; Skelly et al. 1999; Snodgrass et al. 2000; Pechmann et al. 2001; Egan and Paton 2004). Even when mitigation habitats are well designed, adult amphibians often home toward the locations of natal habitats, suggesting the need for active management strategies including translocation and inoculation (Lehtinen and Galatowitsch 2001; Marsh and Trenham 2001).

Other wetland amphibian conservation issues are related to landscape position and biphasic life cycles (aquatic larvae and terrestrial adults). Wetland laws rarely protect terrestrial buffer zones, migration corridors, or surrounding terrestrial habitats, all of which are important for the viability of breeding amphibian populations (Dodd and Cade 1997; Taylor and Scott 1997; Semlitsch 1998; Knutson et al. 1999; Lehtinen et al. 1999; Mazerolle 2001; Houlahan and Findley 2003). For example, the presence of canopied forests reduces dehydration during emigration from breeding sites for many species (Rothhermel and Semlitsch 2002). Next, the population dynamics of species that breed in isolated, depressional habitats are likely to be influenced by metapopulation processes (Fig. 7.9). Spatial distribution of breeding and adult terrestrial habitats at the landscape level may be a more appropriate unit for conservation than an individual wetland (Marsh and Trenham 2001; Trenham et al. 2003). Wetland complexes with a variety of hydroperiods, basin sizes, and canopy covers embedded in a diverse terrestrial matrix are likely to support the highest diversity of wetland amphibians (Pechmann et al. 1989; Knutson et al. 1999; Skelly et al. 1999; Snodgrass et al. 2000).

FIDDLER CRABS

The fiddler crab (*Uca* spp.) is a smallish species (usually <5 cm in length) that has long been a curiosity because males have one oversized claw (that to some resembles a fiddle) used primarily in altercations with other males or to attract females. However, fiddler crabs are one of the ecologically most important animals in salt marshes throughout the world. They can become quite numerous, the larvae are important foods for fish, and the adults are consumed by a host of salt marsh birds (Grimes et al. 1989). To protect themselves

from predators and provide refugia during high tides, fiddler crabs excavate long burrows in salt marsh substrates. The bioturbation caused by burrowing is perhaps the most important impact of fiddler crabs on salt marsh ecology.

In a South Carolina salt marsh, McCraith and associates (2003) found that fiddler crab burrow density ranged from 40 to 300/m², and sediment-reworking rates ranged between 4,400 and 57,000 cm³/m²/yr. Their burrowing mixed the upper layers (8 to 15 cm) of the sediment. This “roto-tilling” and the resultant aeration undoubtedly affects sediment composition and biogeochemical cycles in salt marsh systems. Bioturbation from fiddler crabs can decrease sulfate reduction and increase concentrations of total iron and Fe(III) (Gribsholt et al. 2003). Fe(III) respiration comprised virtually all of the carbon oxidation in bio-perturbed sediments, whereas sulfate reduction was the dominant respiration process in undisturbed sediments (Kostka et al. 2002). However, the impacts of roots from emergent plants such as *Spartina* probably still exceed impacts of fiddler crab burrowing on the overall sediment biogeochemistry in salt marshes (Gribsholt et al. 2003). Nonetheless, fiddler crabs probably merit consideration as ecosystem engineers.

MIDGES

Midges (Diptera: Chironomidae) are small, nondescript flies whose worm-like larvae live in virtually every freshwater wetland. Although noncharismatic, a compelling case can be made that these insects are among the most ecologically important animals in freshwater wetlands. While most animal groups in wetlands are not particularly diverse (Table 7.1), the same can not be said of the chironomid midges. In many if not most wetlands, midges will comprise a large portion of the total animal species richness. For example, researchers have collected 54 midge species from a depression wetland in South Carolina (Leeper and Taylor 1998), 62 species from a Canadian lakeshore marsh (Wrubleski and Rosenberg 1990), 48 species from a rich fen in Canada (Rosenberg et al. 1988), and 51 species from the Florida Everglades (King and Richardson 2002). Midges are notoriously difficult to identify to species, and thus their diversity is probably underestimated in most habitats.

Besides being diverse, midges can reach extremely high population densities. In most wetlands, midges are among the most abundant invertebrates, and densities of more than 10,000 larvae/m² are common (Batzer et al. 1997; Wrubleski 1999). The genus *Chironomus* has fairly large larvae, and when they are abundant, the standing stock biomass can be large (Wrubleski 2005). Midges tend to develop rapidly, and in many habitats, midge species have multiple generations per year. Thus, standing stocks at any particular time may vastly underestimate annual midge production.

It is commonly said that invertebrates in wetlands are the primary link between plant primary production and higher trophic levels (Batzer and Wissinger 1996). This statement may be especially true for midges. Midges are important consumers of plant material, consuming algae and macrophyte detritus (Batzer and Resh 1991; Campeau et al. 1994; Batzer 1998). Midges are then consumed by a wide array of wetland predators. Important invertebrate



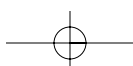
predators of midges in wetlands include dragonflies, beetles, and leeches (Rasmussen and Downing 1988; Batzer and Resh 1991). In a study of a New York marsh, virtually every fish examined, regardless of species, was found to have midge larvae in its guts (Batzer et al. 2000). Many adult ducks consume invertebrates when they need protein to prepare for reproduction or migration, and midges are the mostly commonly consumed taxon (Murkin and Batt 1987; Batzer et al. 1993). Newly hatched ducklings also require invertebrate foods, and these inept predators find midge adults emerging from pupae at the water's surface to be easy prey (Chura 1961). Swallows similarly scoop up midges as they emerge. Midges in general seem almost defenseless to predation, and the key to their success is to reproductively overwhelm the effects of predation. The result is that a large portion of the energy flowing through food webs of freshwater wetlands may be funneled through midges.

In addition to their ecological importance, midges appear to be among the few wetland invertebrates useful for environmental bioassessment. Most invertebrate species in wetlands are ecological generalists, adapted to cope with a range of environmental conditions (Batzer et al. 2004); this tolerance probably makes them poorly suited as environmental indicator species. However, many midges are more specialized, perhaps because the diverse nature of the group forces more niche differentiation. King and Richardson (2002) found that the absence of specific midge species indicated habitat impairment in the Florida Everglades. Mouthpart deformities of midges are also a useful indicator of sublethal effects of pollutants (Dermott 1991).

CADDISFLIES

Larval caddisflies (Trichoptera) live in a wide range of wetland habitats (Wiggins 1973, 1996). The tiny microcaddisflies (Hydroptilidae) and several families of large-bodied case makers (Lepistomatidae, Leptoceridae, Molannidae, and Sericostomatidae) are lentic generalists, occurring in both permanent wetlands and the littoral zone of lakes and ponds. In contrast, temporary-habitat species of net-tube makers (Polycentropidae), northern case makers (Limnephilidae), and giant case makers (Phryganeidae) are wetland specialists with life cycles tailored to the intermittent surface water that typifies many wetlands. Species compositions shift from permanent to semipermanent to temporary wetlands (Wissinger et al. 2003), and this shift in part reflects the absence of desiccation tolerant stages or strategies in permanent habitat species. Species replacements are also the result of trade-offs between traits that facilitate timely emergence from drying habitats (e.g., high activity rates) and traits that facilitate coexistence with permanent-habitat predators (risk-sensitive, low activity rates; Wissinger et al. 1999a, 2003).

Limnephilids in particular possess a suite of life cycle adaptations for life in temporary wetlands including (1) rapid larval growth timed to the seasonal presence of surface water; (2) adult diapause in adjacent terrestrial habitats when wetlands are dry; (3) the deposition of desiccation-tolerant egg masses in dry wetland basins; and (4) larval emergence from protective egg masses only after wetland basins refill (Wiggins 1973; Wiggins et al. 1980;



Richardson and Mackay 1984; Wissinger et al. 2003). *Isonychia plattensis* has the unique trait of crawling from drying basins into adjacent uplands habitats to pupate (Whiles et al. 1999). Because of the importance of the terrestrial adult diapause stage, many wetland caddisflies are probably sensitive to changes in land use in adjacent terrestrial habitats, suggesting the need for protecting terrestrial buffer zones around wetlands.

Limnephilid caddisflies are thought to be *the* most important detritivores in many wetlands (Wissinger 1999). The onset of larval development in many limnephilids is triggered by autumn refilling of basins and coincides with the pulse of detritus from terrestrial leaf fall and the senescence of wetland plants. The diets of many limnephilids are dominated by detritus (Berte and Pritchard 1986; Mihuc and Toetz 1994; Whiles et al. 1999; Wissinger et al. 2003), but compared with stream-inhabiting caddisflies (e.g., Jacobsen and Friberg 1995; Graca et al. 2001), the effects on detritus decomposition in wetlands has been poorly documented (Barlocher et al. 1978; Mackay and Wiggins 1979). Detritus is often a nutritionally incomplete food source (Fig. 7.2), and many detritivorous caddisflies supplement their diets with animal material (Winterbourn 1971; Anderson 1976; Mackay and Wiggins 1979; Berté and Pritchard 1986; Giller and Sangpradub 1993; Wissinger et al. 2004b), including that derived from cannibalism (Wissinger et al. 2006). This protein supplement should accelerate growth and enable escape from rapidly drying habitats.

A distinctive feature of most wetland caddisfly larvae is a portable case fashioned from silk and plant or mineral matter. Several explanations for the evolution of case building are of particular relevance to wetland habitats. Cases protect caddisfly larvae from predators such as fish, salamanders, and invertebrates (Otto and Svensson 1980; Johansson and Johansson 1992; Wissinger et al. 2004a, 2006). Cases also enhance oxygen exchange; wetland species will undulate their abdomen to create currents through the case (Wiggins 1973, 1996; Williams et al. 1987). Finally, cases can reduce the vulnerability of larvae and/or pupae to desiccation and/or freezing (Otto 1983; Zamora-Munoz and Svensson 1996).

Despite having protective cases, wetland caddisfly larvae are eaten by many predators (Johansson and Nilsson 1992; Wissinger et al. 1999a, 2006). Because caddisflies feed heavily on detritus and periphyton, and often comprise much of the invertebrate biomass in wetlands, they are probably important links between primary production and higher trophic levels (Whiles et al. 1999). Moreover, adults provide food for fish, frogs, and insectivorous birds. There is a clear need for experimental research to complement comparative and anecdotal evidence for the trophic importance of caddisflies in wetlands both as primary consumers of detritus and algae and as important conduits of secondary production up through wetland webs.

Invertebrates are widely used for stream bioassessment programs, and three insect orders, the Ephemeroptera, Plecoptera, and Trichoptera (collectively referred to as the EPT taxa), are considered environmentally most sensitive (Karr and Chu 1999). Because wetland caddisflies are strongly influenced by water quality (oxygen), hydroperiod, and riparian conditions, and are also so important ecologically, they are probably a group that merits more research attention for wetland bioassessment (Wilcox et al. 2002).