6 Diversity and Ecology of Vernal Pool Invertebrates

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Hundreds of invertebrate species can be found in vernal pools across northeastern North America — a dramatic contrast to the more than dozen or so amphibians, handful of reptiles, and few opportunistic bird and mammal species that breed, feed, or water in pools. Many invertebrates are temporary water specialists that occur in no other habitats and thus represent important components of local and regional biodiversity. Some are rare or endangered. Ecologically, invertebrates are key to energy and nutrient cycling in vernal pools and play important roles throughout the food web, both as prey and predators. Additionally, invertebrates provide innumerable examples of adaptation and beauty. Changes in hydrology, water quality, vegetation, and light, as well as the introduction of new species, all can profoundly alter invertebrate communities in vernal pools.

The best known pool invertebrates are large crustaceans — fairy, clam, and tadpole shrimp — and aquatic insects, especially larval caddisflies, damsel and dragonfly nymphs, and mosquitoes. These represent only a fraction of the fauna. Less well-recognized, but equally important ecologically, are rotifers, gastrotrichs, worms (flatworms, roundworms, horsehair worms, aquatic earthworms, and leeches), small crustaceans (water fleas, copepods, and ostracodes), molluscs (snails and fingernail clams), arachnids (water mites and spiders), and a wide variety of aquatic insects (including water beetles and bugs, and many kinds of two-winged flies) (Williams 2006) (Color Figure XX*). We generally lack adequate information on distribution and trends in abundance for even the best known of the invertebrates found in vernal pools, such as fairy shrimp (Belk et al. 1998, Jass and Klausmeier 2000).

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Vernal pools with different hydroperiods and patterns of flooding typically contain different, though often closely related, species of invertebrates (Wiggins et al. 1980, Williams 1997, Colburn 2004). Thus, a landscape containing a cluster of pools with different hydrogeological characteristics (see Chapter 2, Rheinhardt and Hollands, and Chapter 3, Leibowitz and Brooks) is likely to support a greater overall richness of invertebrates and to contribute more to regional biodiversity than a single pool or series of similar pools. Unfortunately, many studies of animal life in vernal pools identify invertebrates only to the level of genus and often only to family or order, so that the true diversity represented by vernal pool invertebrates goes unrecognized (Figure 6.1).

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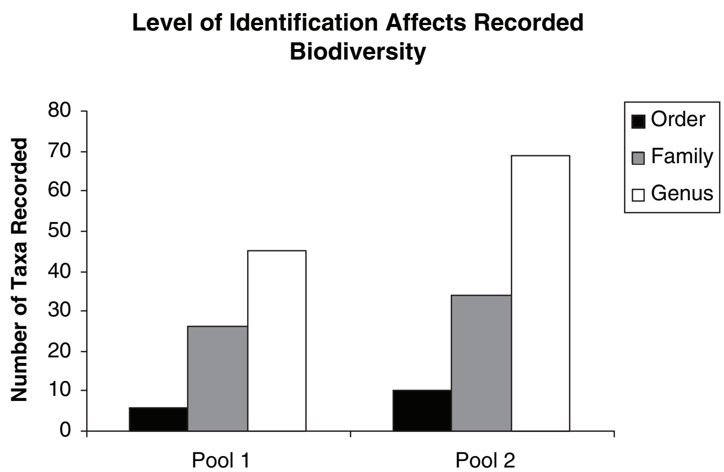

FIGURE 6.1 Comparative data from 2 New England vernal pools sampled in 1997, illustrating how the taxonomic level to which animals are identified influences the measured biodiversity (richness). (From E.A. Colburn, unpublished data.)

In this chapter, we look at general patterns and trends in the distributions and ecology of invertebrates in vernal pools. First, we review invertebrate life-history strategies and community ecology in the context of pool habitat characteristics, especially hydrology. In many cases ecological patterns are suggested by studies carried out elsewhere; there is a need for fundamental ecological work on vernal pool invertebrates in the glaciated Northeast. Next, we briefly introduce some of the most characteristic groups and species, especially those that are restricted to vernal pools and have particularly interesting adaptations and life histories. Finally, we discuss conservation issues and make recommendations based on what is known about the ecology of vernal pool invertebrates. For more in-depth taxonomic and life history details, readers are referred to the cited literature and Colburn (2004).

INVERTEBRATE DISTRIBUTIONS, LIFE HISTORIES, AND DISPERSAL

Factors Influencing Invertebrate Distributions and Life Cycles

A commonly cited benefit of life in vernal pools is the release from predation (and competition) from fish and invertebrates that cannot withstand drying (Williams 1997). This relative freedom from predators allows pool inhabitants unprecedented access to the abundant detrital and algal food (Bärlocher et al. 1978). Vernal pools are not predator-free, however, and some pool invertebrates' life histories and behavior may be tailored to avoid predation (Soderstrom and Nilsson 1972, Schneider and Frost 1996, Brendonck et al. 2002). For example, fairy shrimp (*Eubranchipus* spp.) mature, drop their eggs on the pool bottom, and die by late spring before the water warms, oxygen levels decline, and predaceous salamander and beetle larvae become abundant. The dry eggs overwinter and hatch the following spring. Young *Stagnicola*

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elodes (snails) adapt to pool drying by climbing shrubs and trees to aestivate; they return to the pools in fall. This behavior may help the snails avoid parasitism by sciomyzid fly larvae (Jokinen 1978). Similarly, predator life cycles may track prey populations. The complexity of such interactions highlights how pool alterations can have unexpected ecological effects (see below).

The distributions and trophic relationships of aquatic invertebrates vary with physical substrate, vegetation, and food; changes in any of these may alter the community (e.g., Merritt and Cummins 1996). For example, herbivores are more likely to occur in vernal pools with open canopies, abundant vegetation, and algal growth than in small, closed-canopy pools where the main food source is detritus from annual leaf fall.

Habitat variables are strong drivers of invertebrate life histories in vernal pools and may be especially important for rare species. Every species must deal with pool drying and the between-year variability in timing of pool filling and total pool duration. Some species, especially molluscs, are sensitive to calcium and pH and do not occur in pools where these are low. Many pools freeze solid in winter, precluding those species lacking freeze-tolerant life stages. Summer produces high daily and seasonal temperature variations. Turbidity and seasonally high solute concentrations, low dissolved oxygen, and variable pH can pose problems for some aquatic species (Williams 1987).

Life History Strategies of Vernal Pool Invertebrates

Understanding the wide range of ways that animals deal with complex environmental conditions will contribute to an appreciation of year-to-year variations in community composition in vernal pools. The variety of strategies also illustrates how changes in habitat associated with development or other human activities can have a range of effects, depending on the species involved and the habitat characteristics that are altered.

Because hydrology is ephemeral, or least highly variable (see Chapter 3, Leibowitz and Brooks), vernal pool invertebrates need to start their lives quickly and complete the aquatic portions of their life cycles rapidly (Williams 1987). Such conditions select for two general life history strategies: (1) "early colonization," so that animals can move into new sites wherever conditions are favorable, and (2) "drying response," i.e., an ability to avoid, resist, or tolerate pool drying (Wiggins et al. 1980; Williams 1996, 1997).

Many animals are permanent residents that remain in the pool sediments and become active as soon as water appears and when other conditions (e.g., temperature) are suitable. Some, including mollusks such as the fingernail clam (*Sphaerium occidentale*), burrow into the mud and become dormant as juveniles or adults. Others hatch from desiccation-resistant eggs that can lie in the sediment for months and, in some cases, up to decades, serving as what is known as an "egg bank" (e.g., many crustaceans, including the common fairy shrimps *Eubranchipus neglectus* in the Midwest, *E. vernalis* in the East, and *E. bundyi* in the North).

Dormancy that begins only when pools start to dry allows some permanent residents, such as the water flea (*Daphnia pulex*) or the pond snail *Fossaria* *modicella*, to grow and reproduce as long as water is present. Other species have an obligatory dormant period. Rapid growth and early transformation to adults is seen in many pool inhabitants. The lives of some pool insects include a mixture of short aquatic phases, drought-resistant terrestrial adults, and eggs that resist drying for a few months (e.g., the mosquito *Ochlerotatus* [formerly *Aedes*] *excrucians* and the "log-cabin caddisfly," *Limnephilus indivisus*) (see Chapter 6 and Chapter 9 in Colburn 2004).

Like amphibians, many mobile aquatic insects are migrants that use vernal pools only seasonally. Mosquitoes in the genus *Culex* overwinter as terrestrial adults and migrate to flooded pools in spring to lay their eggs. Water boatmen, backswimmers, and some predaceous diving beetles migrate between permanent waters where they overwinter and vernal pools where they feed and, in many cases, breed. The larvae of some water mites are parasitic on some of these migrants; they avoid seasonal drying and are dispersed to new pools as their hosts fly first to permanent waters and then to vernal pools in spring and summer.

Life history strategies of animals in vernal pools respond to local habitat variability. For instance, some fairy shrimps' eggs are deposited at a depth level that maximizes the chance that when the eggs are flooded, enough water will be present to let the life cycle be completed before the pool dries. Eggs of many species hatch only when certain cues are present (e.g., average temperature, daylight, osmotic shock, and fill level) (Brendonck 1996, Dodson and Frey 2001). Because such cues are sometimes unreliable, most species with egg banks have a "bet-hedging" strategy: only some eggs hatch at any filling in case the pool dries before the life cycle can be completed (Fryer 1996, Simovich and Hathaway 1997, Ripley et al. 2004). As with the long lives and multiple breeding opportunities of amphibians, these strategies let invertebrates adapt to a range of conditions and contribute to the unique and variable communities in vernal pools.

Dispersal

Vernal pools are isolated from permanent water bodies, yet, once flooded, they are rapidly populated by a variety of aquatic invertebrates. How do these animals colonize the pools? In existing pools, we have seen that many species survive drawdown via eggs or drought-resistant larvae and hatch or become active upon flooding. In contrast, species without stages that can withstand drying or freezing in the sediment colonize vernal pools each year.

In new vernal pools, the sediment lacks an egg bank and other dormant stages. Readily dispersed migratory species, such as flying insects, are the earliest colonizers, finding newly formed and freshly flooded pools in as little as 24 h (Grensted 1939, Williams 1987). Most of the species that, once established, can persist by remaining dormant in the sediment during drawdown tend to be less mobile and are dispersed by wind or water, or carried by larger animals (e.g., fingernail clams and crustacean eggs carried by birds, fairy-shrimp eggs transported by crayfish, and leeches dispersed by turtles) (see Chapter 9, Mitchell et al., and Chapter 6 in Colburn 2004). They arrive more slowly; the rate depending primarily on the distance to the nearest source pool (Maguire 1963). Constructed vernal pools, detention basins, and other impoundments are often colonized in this way. These dispersal mechanisms also regulate recolonization of pools after local populations have been eliminated due to unfavorable hydrology, predation, or other causes (Chapter 3, Leibowitz and Brooks). For these reasons and more, it is important to maintain a mosaic of pools well distributed in the landscape.

BASICS OF INVERTEBRATE COMMUNITY ECOLOGY

Invertebrates represent most of the animal species, numbers, and biomass in land, sea, and freshwater ecosystems, including vernal pools, and their ecological importance is proportional to their numbers (Strayer 2006). They play three major roles in vernal pools: (1) helping to cycle algae and dead plant material into animal life, (2) controlling the populations of other animals by competition and predation, and (3) serving as prey for other animals (Figure 6.2).

The aquatic communities of vernal pools can be relatively complex, with many kinds of animals that exhibit a broad range of ecological interactions and collectively occupy a range of trophic levels within pool food webs (Williams 1987, 1997) (Figure 6.2). Some species eat plants and algae. Most taxa — worms, ostracodes, caddisflies, midges, and mollusks on the pool bottom, and filter-feeding crustaceans and insects in the water — feed on detritus, making large amounts of nourishing food available to the rest of the community (detritus, mainly in the form of leaves from the surrounding forest, constitutes more than 50% of the energy input into vernal pools) (Barlöcher et al. 1978). Others are predators and parasites (see Chapter 13 in Colburn 2004).

Competition and predation strongly structure pool communities. Competition can occur between dramatically divergent taxa. Snails compete with American toad (*Bufo americanus*) tadpoles for algae in streamside pools in Kentucky (Holomuzki and Hemphill 1996). In Europe, cooccurring mosquito larvae and toad tadpoles negatively affect one another (Blaustein and Margalit 1994). Unquestionably, hundreds of interactions occur among members of the aquatic communities in northeastern vernal pools. Equally important are the effects of intraspecific competition on invertebrate growth, reproduction and survival. For example, high intraspecific densities reduce growth in parasitic water mite larvae and clam shrimp and decrease survival in temporary-pool mosquitoes (Lanciani 1976, Gleiser et al. 2000, Weeks and Bernhardt 2004).

Predators such as dragonfly nymphs, diving-beetle larvae, flatworms, and salamander larvae can dramatically affect invertebrate species' abundances and the composition of the entire community (Blaustein et al. 1996, Brendonck et al. 2002, Eitam et al. 2002). Interactions between amphibians and invertebrates, with invertebrates serving as prey in some cases, and as predators in others, are a common and necessary component of normal functioning in vernal pool ecosystems. For instance, egg predation by leeches (Cory and Manion 1953) and giant tube, case-making caddisfly larvae (*Ptilostomis* and *Banksiola* spp.) can influence the hatching success of wood frogs (*Rana sylvatica*) and spotted salamanders (*Ambystoma maculatum*); predation by dragonfly nymphs affects the survival of toads, chorus frogs (*Pseudacris* spp), and salamanders, whereas amphibian larvae consume a wide array

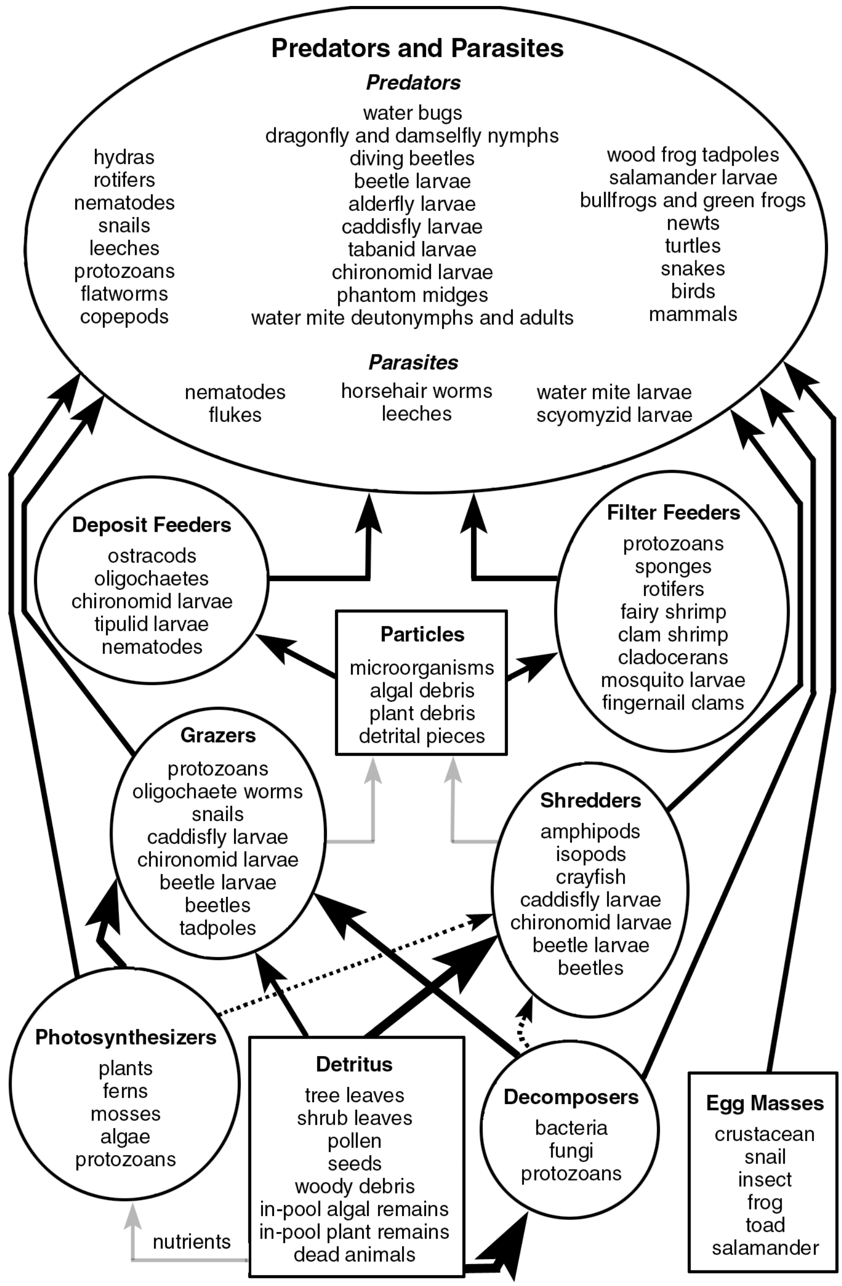

FIGURE 6.2 A generalized vernal-pool food web. Herbivorous grazer/scrapers and filter-feeders feed on algae and living plants; microbes decompose and detritivores consume dead plant and animal materials; and predators and parasites feed on the living animals that are sustained by the rich plant-derived diet of the pool bottom and water column. (From Colburn, E.A. [2004]. *Vernal Pools: Natural History and Conservation*. McDonald and Woodward Publishing Company, Blacksburg, VA. With permission.)

of invertebrate prey (Brockelman 1969, Smith 1983, Stout and Stout 1992, Rowe et al. 1994). In other parts of the world, introduced fish or dragonfly nymphs have disrupted food webs and threatened native species by altering predator–prey relationships in pools (Courtenay and Meffe 1989).

COMMON INVERTEBRATES OF VERNAL POOLS

Large Crustaceans

Six major groups of large crustaceans occupy vernal pools in the northeastern United States and Canada. Typical — and indicative — of temporary waters are fairy shrimp, clam shrimp, and tadpole shrimp (Table 6.1). All are found in temporary waters worldwide, all have similar life-history strategies that include production of resting eggs that lie in the egg bank and hatch upon flooding at a later time, and all "hedge their bets" through staggered hatching (see above). Isopods, amphipods (Color Figure XX), and crayfish occur in a variety of aquatic habitats and are not discussed here.

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Fairy Shrimp (Order: Anostraca)

Among the general public interested in natural history, fairy shrimp are probably the best known of the invertebrates unique to vernal pools. In our region, the common species are in the genus *Eubranchipus*. The eggs typically require cold-conditioning and drying before they will hatch. Once flooded, eggs typically hatch in 1–14 d, depending on temperature. Animals are sexually mature in as few as 2–4 weeks, although maturation can be delayed by colder water temperatures. Fairy shrimp can be recognized by their large size — up to 2 cm (0.8 in.) — and orientation during swimming: they swim "upside down," with their numerous, feathery, plate-like appendages aimed upwards (Color Figure XX). Males are recognized by the enlarged second antennae ("claspers") that are used to grasp females during mating. Females have a clear "brood pouch" in which eggs are held for fertilization and often a bright blue patch near this pouch. Both sexes are typically clear or white but can take on various colors, including blue, red, and orange.

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These interesting crustaceans are primarily filter feeders that consume algae, zooplankton, and even bacteria (Dodson and Frey 2001). They tend to swim up in the water column but will hide in the leaf litter when disturbed. Males actively search for mates and thus are often more conspicuous than females. Because of their inability to avoid fish predators, fairy shrimp are found exclusively in fishless ponds. Also, because eggs require a period of drying, fairy shrimp are not common in semipermanent pools with little fluctuation in water depths. Several species are rare or endangered in our region.

Clam Shrimp (Orders: Laevicaudata, Brevicaudata, and Spinicaudata)

In vernal pools, different species of clam shrimp can be found primarily from early May to mid- September. Many species have restricted distributions and are

TABLE 6.1
Large Branchiopod Species of Vernal Pools, Including Seasonal Information

Genus	Species	Season	Location[a]
A. Fairy shrimp			
Branchinecta	*paludosa*	Su	AB, LB, NS, QB
Eubranchipus	*bundyi*	W, Sp	IL, IN, MA, MI, MN, NH, NY, OH, VT, WI, AB, ON, QB
	intricatus	W, Sp	MA, ME, AB
	ornatus	W, Sp	MN, WI, AB
	holmanii	W, Sp	CT, IL, MN, NJ, NY, OH
	neglectus	W, Sp	IL, IN, MI, OH, ON
	vernalis	W, Sp	CT, MA, ME, NJ, NY, PA, RI
	serratus	W, Sp	IL, IN, OH, WI
Streptocephalus	*sealii*	W, Sp, Su	IL, MN, NJ, NY, AB
B. Clam shrimp			
Lynceus	*brachyurus*	Sp, Su	MA, IL, IN, MI, NH, OH, RI, AB, ON
Cyzicus	*mexicanus*	Su	IL, OH, AB
Caenestheriella	*gynecia*	Su	MA, OH, PA
Limnadia	*lenticularis*	Su	MA
Eulimnadia	*diversa*[1]	Su	IL, IN, MI, OH
	agassizii[2]	Su	CT, MA
C. Tadpole shrimp			
Lepidurus	cousii	W, Sp	MN

Note: W= winter form; Sp = spring form; Su = summer form) and geographic location (by U.S. state/Canadian province within the glaciated Northeast.

[a] Location codes for (1) U.S. states: CT = Connecticut, IL = Illinois, IN = Indiana, MA = Massachusetts, MI = Michigan, MN = Minnesota, NH = New Hampshire, NJ = New Jersey, NY = New York, OH = Ohio, PA = Pennsylvania, RI = Rhode Island, VT = Vermont, WI = Wisconsin; (2) Canadian provinces: AB = Alberta, LB = Labrador, NS = Nova Scotia, ON = Ontario, QB = Quebec. [1]Includes *E. thomsoni* and *E. inflecta*. [2]Includes *E. stoningtonensis*.

considered rare. The bivalved carapace of clam shrimp is either spherical or oval and can be clear to dark brown. Because they look much like small (4–20 mm) clams, they are often misidentified as freshwater bivalves. Some species are easy to overlook, as they tend to be on pool bottoms, where they scavenge among the leaf litter, or are actually slightly buried in the sediment. *Lynceus brachyurus,* a broadly distributed species in vernal pools with an adult diameter of 5 mm, is a filter feeder that swims in the water column. Clam shrimp usually develop faster and have shorter lives than fairy shrimp. Populations either comprise males and females, all females, or males and hermaphrodites (Sassaman 1995).

Tadpole Shrimp (Order: Notostraca)

In our study area, tadpole shrimp have been described only from Minnesota, where *Lepidurus cousii* can be found rooting around pool bottoms (Rogers 2001, D. Batzer, personal communication). They are omnivorous scavengers and opportunistic or facultative predators (Weeks 1990). Superficially resembling amphibian tadpoles or miniature horseshoe crabs, these "living fossils" are generally the largest branchiopods in vernal pools where they occur, reaching lengths of 4 cm.

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Small Crustaceans

Some of the most diverse vernal pool inhabitants are small crustaceans in the classes Ostracoda (seed shrimp) and Copepoda (copepods), and the Order Anomola (cladocerans, or water fleas) (for details and species lists, see Colburn 2004) (Color Figure XX). All 3 groups are found worldwide. Most are filter feeders and detritivores, but they include a broad diversity of ecological types. All are important prey for other animals in vernal pools, and all contribute desiccation-resistant eggs to the egg bank. Many species are undescribed (King et al. 1996).

Ostracodes (Order: Podocopida)

Ostracodes are small, bivalved, benthic crustaceans with a spherical, ovoid, or elongate-cylindrical shape. They look much like white, brown, green, or purple sesame seeds, reaching ~2 mm in length in our region. Ostracodes are the oldest microcrustaceans known (Delorme 2001) with at least 29 species associated with vernal pools, where they are scavengers, herbivores, and detritivores in the sediment.

Copepods (Class:Copepoda)

Copepods constitute the most diverse group of the microcrustaceans, with over 10,000 described species (Williamson and Reid 2001). At least 16 species are found in vernal pools. Copepods are cylindrical to tear-drop-shaped, with a long, bifurcated tail with several setae, and with two antennae used in some species for rapid swimming (Plate xx). They can be planktonic or benthic and include filter feeders, omnivores, and carnivores. Some diaptomid copepods reach several millimeters in length, are bright blue, and are readily visible as they swim upside-down in the water column in early spring.

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Water Fleas (Order: Anomola)

Water fleas, or cladocerans, are small (generally <5 mm), planktonic or benthic microcrustaceans (Color Figure XX). At least 17 species have been reported from vernal pools. Most are filter feeders, using their plate-like appendages to create currents within their bivalved carapaces from which they filter out small food particles. Ironically, when food becomes superabundant, water fleas can starve because the energy required to clean their filtration apparatus is greater than their food intake (Dodson and Frey 2001). Cladocerans are clear to a yellowish color and swim in jerky, small jumps. They either brood live young under their carapace or produce desiccation-resistant eggs (ephippia) that will lie dormant in the egg bank until conditions are favorable for hatching. Many of these crustaceans reproduce via "cyclic parthenogenesis," wherein all-female populations reproduce asexually for most of their lives, and then produce males and reproduce sexually (producing the ephippia) as the pond is finally drying up. *Daphnia pulex*, commonly studied in biology courses, is widely distributed and abundant in vernal pools.

Flatworms and oligochaetes: Vernal pools support a wide variety of worms from several phyla, including Platyhelminthes (flatworms), Annelida (leeches and earthworm-like segmented worms), Nematoda (roundworms), and Nematomorpha (horsehair worms). Worms play key roles in vernal pools as predators, scavengers, and detritovores (for more information on worms in vernal pools, see Colburn 2004).

Free-Living Flatworms (Class: Turbellaria)

Related to the *Planaria* that most people see in biology classes, but usually without the distinctive triangular head, the dozen or so species of vernal-pool flatworms are small (mostly < 5 mm long and 1–2 mm wide), flattened, drably colored (coming in grays, light browns, pale pinks and, in one species, bright lime green), and slow-moving; they tend to remain hidden under leaves on the pool bottom (Color Figure XX). They are permanent residents that survive pool drying by fragmenting into a series of small pieces that become hardened and resist drying until the pool refloods and water temperatures are low. Flatworms are cold-water specialists. Best observed in vernal pools in winter or early spring, they are important predators and scavengers (Kenk 1949, Wiggins et al. 1980, Ball et al. 1981).

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Oligochaetes (Class: Oligochaeta)

Oligochaetes in vernal pools look like small, freshwater earthworms. As on land, they are key to energy cycling: they ingest sediment, absorb nutrients, and produce castings that are then colonized by microbial decomposers and grazed by other animals, including amphibian tadpoles. They are found in the decomposing leaves on the pool bottom, and in late summer or fall they are among the most abundant animals living in the wet pool substrate. To survive pool drying, these worms fragment into cysts, encase themselves in a coat of protective mucus, or deposit eggs in desiccation-resistant cocoons (Kenk 1949, Wiggins et al. 1980).

Mollusks

Air-breathing snails and fingernail clams (also known as pill clams) are common in many vernal pools. Their shells on a dry pool bottom indicate the seasonal presence of water there.

Snails (Class Gastropoda, Order Basomatophora)

Gilled snails with opercula that close off the shell do not occur in vernal pools; all of the snails in pools are pulmonates, or air-breathers. Most of the 19 species reported from vernal pools occur widely in floodplains and other kinds of wetlands, but the common stagnicola (*Stagnicola elodes*), the polished tadpole snail (*Aplexa elongata*), and the toothed planorbid (*Planorbula armigera*) are especially characteristic of vernal pools (see Chapter 7 in Colburn 2004).

Snails often hang upside-down from the water's surface, taking air into the mantle cavity, from which they absorb oxygen into their blood. Most are grazers, feeding on algae, aquatic plants, dead plant and animal matter, and small organic particles on the water's surface and pool bottom. However, the common stagnicola is a predator, feeding on mosquito larvae and other prey. Snails are preyed upon by a variety of invertebrates and vertebrates and are hosts for parasitic flukes — including species that parasitize amphibians — and sciomyzid fly larvae.

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When vernal pools dry, most snails aestivate by secreting a mucus membrane across their shell opening and burrowing into the sediment, where relative humidity remains high. Some species only resist drying as juveniles, whereas others can do so as adults. Most snails can grow for as long as water is available. High reproductive output and continuous growth help compensate for naturally high juvenile mortality in these seasonally drying habitats. When pools flood, animals emerge from the mud, feed, grow, mature, mate (they are hermaphroditic and can mate with any other individual), and lay eggs. They may produce several broods during a single season. Young snails hatch directly and start at once to feed and grow. The cycle continues until pool drying.

Fingernail Clams (Class: Bivalvia)

Fingernail clams are so-called because their adult size is about that of a human fingernail. They are highly efficient filter-feeders (McMahon and Bogan 2001) and, unlike freshwater mussels which have a mobile aquatic larva, they bear live young that are released as miniature replicas of their parents. Four of the 5 common species occur in a wide range of habitats, but Herrington's fingernail clam (*Sphaerium occidentale*) is a vernal-pool specialist.

Like snails, fingernail clams survive pool drying by remaining dormant in the pool sediment. Broadly distributed, species of *Musculium* and *Sphaerium* can resist drying only as newly hatched juveniles. They emerge in spring-filling pools as waters start to warm, feeding and growing until ready to reproduce, and releasing young that immediately enter summer diapause. Mature individuals continue to feed and produce young until pool drying, when they die. In fall-filling pools, young may emerge from diapause and grow until temperatures become cold, resuming growth in spring. In contrast, the vernal pool-specialist Herrington's fingernail clam tolerates drying in all life stages and thus can feed and grow continuously from hatching until pool drying. It produces more young than other fingernail clams found in vernal pools and lives for 3 years, as opposed to a 1-year lifespan for most other species, and thus can compensate for high juvenile mortality and a short growing season in short-hydroperiod pools (Heard 1977; Mackie 1979; McKee and Mackie 1980, 1981).

Aquatic Insects

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Hundreds of species of aquatic insects occur in vernal pools, including members of the orders Trichoptera (caddisflies), Coleoptera (water beetles), Odonata (dragonflies and damselflies), Hemiptera (water bugs), and Diptera (true flies, including midges, crane flies, and horseflies). Each common order contains multiple genera and species. Some may be widely distributed in vernal pools, whereas others are quite localized. Ephemeroptera (mayflies) (Color Figure XX), Plecoptera (stoneflies), and Megaloptera (alderflies) are relatively uncommon in vernal pools and will not be addressed here. Of all the insects found in vernal pools, mosquitoes (Order Diptera, Family Culicidae) have the greatest potential influence on the conservation of vernal pools due to their links to public health and strong public and governmental sentiment in favor of destroying breeding habitats.

Caddisflies (Order: Trichoptera)

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Caddisflies are aquatic as larvae and pupae. Many are easily recognized by the cases or retreats they construct with silk and either pebbles, sticks, or leaves (). The cases (Color Figure XX) represent an important adaptation for life in nonflowing waters such as ponds and wetlands, allowing the larvae to create water currents that increase oxygen flow (Wiggins 1996). The larvae have three pairs of legs; elongate, cylindrical bodies; soft, thin-skinned abdomens; a thickened head; and a hardened plate on the first thoracic segment. A pair of prolegs, each with a claw-like hook, is found at the end of the abdomen. Like moths and butterflies, adults hold their wings together above the body when at rest. Caddisfly larvae are highly diverse in their feeding strategies and include shredder-detritivores, shredder-herbivores, collector-gatherers, collector-filterers, scrapers, and engulfer-predators. The most common caddisflies in vernal pools have adults that diapause during hot, dry periods, later emerging to produce eggs that resist drying on the pool bottom until flooded. Larvae are found in vernal pools around 1–3 d after flooding, and adults emerge in late spring/early summer, depending on the species (Wiggins 1973). The empty cases on the dry bottom provide evidence during drawdown of a pool's existence.

Aquatic Beetles (Order: Coleoptera)

The water beetles are in the largest order of insects and can be found in just about any vernal pool sampled. They include species of whirligig beetles that swim on the surface, predaceous diving beetles (some with fierce larvae known as "water tigers"), water scavenger beetles, crawling water beetles, minute moss beetles, snout beetles, and others. They comprise shredder-herbivores, collector-gatherers, collector-filterers, scrapers, and engulfer-predators. Water beetles are aquatic as larvae and adults but pupate on land. The larvae have three pairs of legs; thick, hardened skin on their head; and, often, large pincer-like mandibles. In adults, the front wings are modified into hard plates or "elytra" that cover the hind wings and abdomen.

Some adults diapause in the substrate when pools dry. Others are migrants and arrive in vernal pools anywhere from just a few days after pond filling to several weeks later, and they may remain present until drawdown (Williams 1987). A few water beetles have diapausing eggs, but most species' larvae appear after eggs are laid in the water by resident adults or by adults dispersing into the vernal pool to breed (Wiggins et al. 1980). Beetles show some of the greatest overall biodiversity in vernal pools, and their distributions may vary with forest composition and other local factors. Some species are restricted to vernal pool habitats, and some may be rare.

True Bugs (Order: Hemiptera)

True bugs include backswimmers, water boatmen, giant water bugs, creeping water bugs, water striders, water scorpions, and marsh treaders. Nymphs and adults occur in the same habitat. Nymphs look like adults with undeveloped wings. The mouthparts are modified into a cone or beak, and each leg has two claws. All are piercer-predators (except for the water boatmen, most of which are collector-gatherers) that feed on other invertebrates and on larval amphibians. Hemipterans do not undergo egg diapause; most are migratory. Eggs are laid when adults arrive at the pools and hatch within 1–2 weeks; nymphs grow rapidly in order to be ready to fly from the pool before it dries (Voshell 2002).

Damselflies and Dragonflies (Order: Odonata)

Damselflies and dragonflies are aquatic only as nymphs. They are recognized by the long lower lip (labium) that folds back against the head and is used as a powerful pincer to capture prey. plate-like gills extending from the end of the abdomen. The colorful adults have very long abdomens and large heads and eyes. Dragonflies hold their wings out to the sides of their body when at rest and damselflies hold them together, or nearly so (i.e., *Lestes* spp.), above the body.

All odonates are engulfer-predators. Adults of some species, such as the common green darner (*Anax junius*), migrate from the south to breed in vernal pools. In others, the females lay diapausing eggs in aquatic plants or on the pool bottom, and the eggs remain dormant until the next pond filling (Wiggins et al. 1980, Voshell 2002). Closely related species may occur in adjacent pools with different hydrologic regimes.

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True Flies, Exclusive of Mosquitoes (Order: Diptera)

The true or two-winged flies include the mosquitoes (see below), midges, phantom midges (see Color Figure XX), craneflies, horseflies, marsh flies, and common flies. In water-dependent groups, larvae and pupae are aquatic, and adults are terrestrial. Unlike other insects found in vernal pools, the larvae of true flies lack segmented legs. The thorax and abdomen are soft and thin-skinned, and the head is either continuous with the thorax or thick skinned and separated from the thorax. The diversity of this group also equates to diverse distributions and ecology. Most dipterans are collector-gatherers, but some are scrapers, shredder-detritivores, and engulfer-predators. They can undergo long egg diapause during the dry period, and eggs hatch just a few days after the vernal pool is hydrated (Voshell 2002).

Mosquitoes (Order: Diptera)

The best known (and least loved) dipterans are the mosquitoes (family Culicidae). About 30 species have been identified from vernal pools (see Colburn 2004). The eggs of many species overwinter in the sediment and hatch when flooded, but *Culex* females overwinter as adults and lay their eggs in spring on the water's surface. In early spring, mosquito larvae are present in the thousands in some vernal pools. They eat decaying material, microorganisms, pollen, and small particles on the surface or in the water. They are fed upon by snails, bugs, copepods, beetle larvae, caddisflies, phantom midges, odonate nymphs, newts, and salamander larvae; fewer than one percent of larvae survive to adulthood (Collins and Washino 1985).

Like all dipterans, the aquatic larvae are legless. They have a round head, a swollen thorax, bristly hairs all over their bodies, and typically a tubular siphon at the end of the abdomen through which they obtain air at the water's surface, where the larvae tend to congregate. When disturbed, larvae ("wrigglers") thrash about. After going through several molts, larvae transform into pupae ("tumblers"), which are somewhat comma shaped, with a large swollen upper end containing the head, upper body, a pair of horn-like breathing tubes, legs, and developing wings; the narrow abdomen extends below. Once the body has been reorganized, the pupal skin splits and the adult emerges. Only females bite: the blood meal provides protein that is used to produce eggs. Depending on the species, females lay their eggs on the water's surface or on the damp substrate of a drawn-down pool.

In our geographic region, mosquitoes are largely nuisances that annoy humans with their buzzing and cause discomfort but no lasting harm with their bites. However, two mosquito-borne diseases, West Nile virus (WNV) and eastern equine encephalitis (EEE), are of public health concern and have important implications for vernal pools. These are primarily viral diseases of birds, but they can be transmitted to horses, humans, and other mammals by mosquitoes that have bitten an infected bird. From both EEE and WNV, birds suffer the most illness and mortality.

Because EEE and WNV are transmitted by mosquitoes, there is a major focus on controlling mosquito populations, and because mosquitoes are a substantial part of the fauna of vernal pools, these habitats are vulnerable to mosquito control activities. However, both EEE and WNV are transmitted to humans only if a mosquito first bites an infected bird. Most mosquito species found in vernal pools do not feed on birds (and most do not feed on humans, either, although some important pest species do breed in vernal pools). The most common mosquito transmitting EEE is *Culiseta melanura,* which breeds preferentially in hardwood swamps and is not commonly found in vernal pools. The most common vectors of WNV are *Culex* spp., which similarly are not common in vernal pools. However, more than 60 species of mosquito are known to carry WNV, and some of the common species from vernal pools have tested positive for WNV (Center for Disease Control and Prevention 2006a, 2006b). Note that mosquito control activities usually involve altering hydrology, introducing predators, and/or applying pesticides to breeding areas. Therefore, diverse food webs, sensitive faunas, and long-term community viability (including the viability of natural mosquito predators) are at risk if mosquito-control efforts focus on vernal pools.

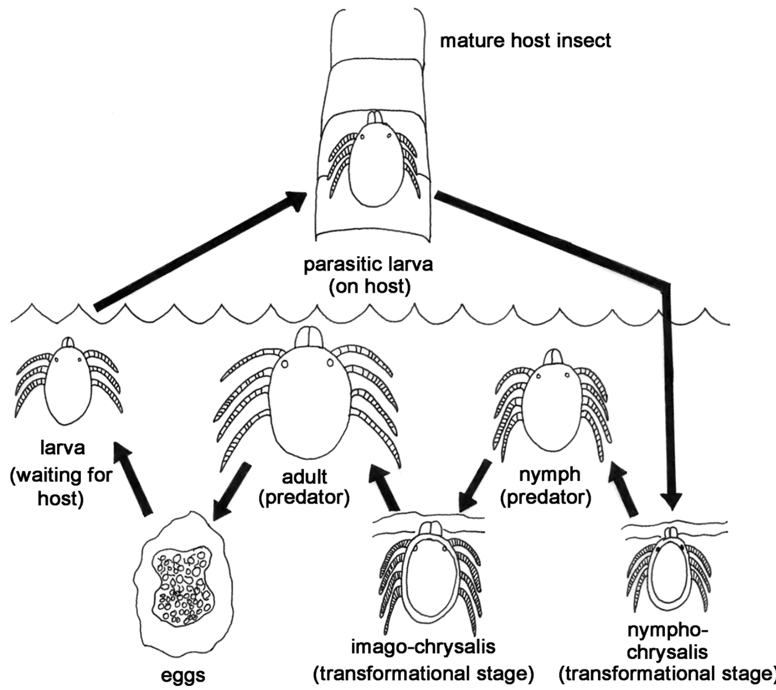

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FIGURE 6.3 Generalized life history of water mites in vernal pools. (From Smith et al. 1997. With permission.)

Water Mites

Around 50 species of water mites (Acari) are known from vernal pools, and there are probably more. These tiny (usually < 5 mm), round, seemingly headless, 8-legged animals; they come in reds, yellows, greens, blues, and browns, and can be observed crawling on the substrate and swimming in the water. As larvae, they parasitize adult aquatic insects (Figure 6.3). Some are attached to their hosts as the latter fly around the pools seeking food or mates. These parasites can be so dense that they affect the hosts' ability to fly and reproduce. Once fed, the larvae drop off of the hosts and back into the pool, where they transform into nymphs that prey on the eggs of crustaceans or insects, or on insect larvae (especially midges and mosquitoes). The nymphs transform into predatory adults. Unless they migrate as parasitic larvae attached to hosts, water mites withstand pool drying as dormant adults or nymphs. We recommend interested readers to additional information in Smith et al. (2001).

SUMMARY

Aquatic macroinvertebrates make up most of the animal species and biomass in vernal pools. Because the species that occur in short-duration pools are different from those in pools with longer hydroperiods, and because vernal pool species differ from those in permanent waters, pool invertebrates contribute significantly to local and regional biodiversity. They play key roles in the transfer of energy from leaves and other detritus into animal biomass, serve as food for vertebrate predators (including turtles and salamander larvae), and structure the populations of other species (including amphibians) by predation and competition. Their life cycles are complex and closely related to hydroperiod and other habitat variables. Some species can grow and develop whenever conditions are favorable. For others, highly specific cues of temperature, water level, and chemistry stimulate hatching, growth, and maturation. The wide variety of strategies for dealing with seasonal pool drying ranges from egg banks, in which dormant cysts remain viable for decades, to facultative dispersal from permanent waters into flooded pools for feeding and breeding. The protection and maintenance of a diverse habitat mosaic of vernal pools with a range of hydroperiods and other physical conditions is key to the long-term conservation of vernal pool invertebrate communities.

CONSERVATION IMPLICATIONS AND RECOMMENDATIONS

Because invertebrate distributions and life cycles are closely tied to habitat variables (such as hydrology, water quality, and both in-pool and surrounding vegetation), activities that alter any of these variables have the potential to alter invertebrate communities. Inadequate knowledge of the species in vernal pools and of their interrelationships means that there is a risk of losing rare species and altering community dynamics as pools and their watersheds are altered by human activities. Natural year-to-year variability in weather and pool characteristics, and the high plasticity of invertebrate life cycles, make it difficult to evaluate the effects of human alterations, especially subtle changes over time.

Various factors threaten invertebrates in vernal pools. Direct threats include: ditching and pesticide use for mosquito control; filling; excavation for detention basins, fish ponds, mosquito control, and wildlife habitat enhancement; sedimentation; and chemical contamination from runoff. Less direct but potentially serious threats include altered hydrology, water quality, and food associated with changes in watershed land use or cover, atmospheric deposition, and climate change. Many of these, such as pool destruction and watershed activities that alter hydrology or water quality, affect both vertebrates and invertebrates. Alterations of forest composition, whether through forestry, clearing for development, or natural succession can change inputs of light and leaf litter, affecting the base energy sources for pools and the invertebrate communities therein.

Below, we comment briefly on several threats that we believe specifically affect invertebrates in vernal pools. Additionally, best management practices for forestry (Chapter 13, deMaynadier and Houlahan) and development (Chapter 12, Windmiller and Calhoun), to the extent they maintain water quality, hydrology, and natural vegetation adjacent to pools, will also benefit invertebrate conservation.

Pool Protection Efforts

A wide range of hydroperiods in temporary waters contributes to aquatic biodiversity. In particular, although small, short-duration pools tend to support fewer species, they also tend to support taxa that do not occur or reproduce successfully in longer-hydroperiod pools. Conservation efforts often explicitly exclude small, short-duration pools because relatively fewer amphibian species breed in such pools compared to longer-hydroperiod, annual and semipermanent pools, and because there has been speculation (with little empirical evidence) that short-hydroperiod pools are sinks in which amphibian breeding effort is wasted. This is problematic from the perspective of invertebrate biodiversity. We suggest that the full range of pool sizes and hydroperiods needs to be protected to ensure the maintenance of regional biodiversity and the persistence of invertebrate metapopulations.

Habitat Enhancement and Aesthetics

Some efforts to enhance the value of vernal pools for amphibian populations, especially mole salamanders (*Ambystoma* spp), have involved dredging annual pools to increase their hydroperiods, even to the extent of changing them to permanent or semipermanent pools (Colburn, personal observation). Additionally, many vernal pools are excavated by individual property owners to create "water features" in gardens, to eliminate the unsightly appearance that many pools take on in the summer, and/or to allow the stocking of ornamental fishes such as koi (*Cyprinus carpio*) or of frogs such as bullfrogs (*Rana catesbiana*), which are readily available from some garden centers. Such activities are of concern from several perspectives.

First, excavation of the substrate removes the egg bank to which many generations of permanent-resident crustaceans and other invertebrates have contributed. It also removes insect eggs, dormant cysts of flatworms and oligochaetes, aestivating mollusks, and a host of other species. Even if some individuals should persist, the process would likely significantly reduce the genetic diversity of local populations, very possibly dooming many of them to local extirpation. Some of the lost taxa may be important food sources for the very amphibians that are the target of conservation.

Second, by increasing the hydroperiod, and especially by eliminating regular drying, the pool is made potentially hospitable to long-lived, drought-intolerant predators commonly excluded from seasonally drying pools, including several species of dragonfly nymphs, backswimmers, giant water bugs, and predaceous diving beetles. These predators are more widely distributed than many of the taxa typical of short-duration pools and are less likely to be restricted to vernal-pool habitats. They may exclude invertebrate taxa that originally inhabited the pool, and they may prey on larvae of vernal pool amphibians, potentially contributing to decreased reproductive success over time — an effect opposite to that intended.

Third, stocking of koi, bullfrogs, and other predators can devastate the native invertebrate community. Before more pools are dredged, we believe there is a need for: (1) long-term studies to determine the overall reproductive success of important amphibian populations in pools of different hydroperiods, factoring in the normal variability in flooding durations and the large natural variation in numbers of transforming juveniles across years; (2) comparative long-term studies of invertebrate populations (especially predators) and amphibian reproductive success in pools in which hydroperiods have been altered vs. those that are allowed to dry naturally; and (3) a reassessment of management aims for wildlife reserves to determine whether alteration of pool hydroperiods makes good conservation sense from the perspective of both amphibian and invertebrate biodiversity.

Mosquito Control

Ditching, draining, filling, excavation, and the application of pesticides all dramatically alter vernal pool habitats and can adversely affect the entire pool community. Individuals interested in and concerned about vernal pools and their wildlife need to (1) educate their neighbors and public health officials about the larger ecosystem values of vernal pools, (2) engage in public discussions of the relative risks of infection from serious diseases, and of the nuisance aspects of mosquitoes vs. risks to wildlife of mosquito control at individual pools, (3) help to minimize breeding habitats (such as tires, gutters, and open containers) in which *Culex* spp. breed preferentially, and (4) encourage people to use insect repellents, wear long sleeves and pants, and avoid areas where mosquitoes congregate at dawn and dusk.

If mosquito control is absolutely critical for a specific vernal pool, the use of the microbial larvicide *Baccillus thuringiensis* var. *israeliensis* (Bti), which kills mosquito larvae and related flies such as midge larvae, is preferable to ditching, excavation, introduction of fish, or the use of broader spectrum pesticides. However, all of the affected insects are important components of the food web, and removing them can have potentially wide-ranging, unintended ecosystem effects.

Pesticides and Other Chemicals

Invertebrates are often highly sensitive to water chemistry and are good water quality indicators (Rosenberg and Resh 1993). Very little is known about how pollutants affect invertebrates in vernal pools (Chapter 11, Boone and Pauli). For instance, of the hundreds of vernal pool invertebrates, only *Daphnia pulex* is routinely used in bioassays of pesticide effects on "non-target" species. Thus, we cannot predict the overall impacts of common pesticide formulations on pool fauna. Similarly, effects of contaminants in runoff and precipitation are generally unknown.

Public Education

Aquatic invertebrates are fascinating, beautiful, and critically important components of vernal-pool ecosystems. Their diminishment decreases overall biodiversity and weakens the web of life connecting forests, waters, and humans. The loss of upland woods, associated vernal pools, and aquatic biodiversity, is ongoing. To counter it, public awareness and appreciation of vernal pools and their biota must be greatly enhanced, and substantial areas of intact landscape must be acquired and conserved.

ACKNOWLEDGMENTS

We thank M. Simovich, D. Batzer, A. Calhoun, B. Swartz, P. deMaynadier, and an anonymous reviewer for helpful feedback on earlier drafts of this chapter, and I. M. Smith, J. Semroc, and J. McDonald for permission to use illustrations, and J. Cossey for assistance in production of Color Figure XX.

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