

habitats derive most of their nutrients from detritus (decaying matter) washed into pools from adjacent uplands, and these nutrients provide the foundation for a vernal pool aquatic community's food chain. Detritus is a primary food source for the vernal pool crustaceans addressed in this rule (Eriksen and Belk 1999). Because vernal pools are mostly rain-fed, they tend to have low nutrient levels and dramatic daily fluctuations in pH, dissolved oxygen, and carbon dioxide (Keeley and Zedler 1998).

Both the amount and timing of rainfall in California and Oregon vary greatly from year to year. As a result, pools may fill to different extents at different times. The duration of ponding of vernal pools also varies, and in certain years some pools may not fill at all. Many characteristics of vernal pool plants and animals result from these organisms' adaptations to the highly variable and unpredictable nature of vernal pools (Holland 1976; Holland and Dains 1990; King *et al.* 1996; Hanes and Stromberg 1998).

Compared to vernal pools worldwide, vernal pools in California and Oregon are rich in species composition and contain many species that are endemic to the region (found nowhere else). In addition, while most of California's grasslands are now dominated by nonnative grasses and other introduced plants, vernal pools remain a haven for native species. Invasive nonnative plants have been introduced into California and have spread and reproduced in upland habitats so successfully that it is not unusual for nonnatives to account for a third of the species and more than 90 percent of the biomass in a California grassland. Vernal pools have dramatically resisted this invasion: 75 to 95 percent of plant species found in vernal pools are native, and natives dominate in biomass as well as in number (Holland and Jain 1978; Jokerst 1990; Spencer and Rieseberg 1998). Vernal pool plant communities are able to resist invasion of upland species because of the severe ecological constraints on plants living in vernal pool environments.

The animal communities that live in vernal pools also contain diverse groups of highly specialized species. The freshwater crustacean communities of vernal pools are particularly well developed (Simovich 1998). The most visible crustaceans in vernal pools are the large branchiopods (literally, "gill-foots"), about 27 species in California, of which perhaps 10 are endemic (Helm 1998; Belk and Fugate 2000) and 6 are federally listed as threatened or endangered. The large branchiopods are easily visible to the naked eye, ranging

up to 2 inches (in) (5 centimeters (cm)) in length, depending on the species. They include the fairy shrimps (Anostraca), tadpole shrimps (Notostraca), and clam shrimps (Spinicaudata and Laevicaudata). Smaller crustaceans that are common in California vernal pools, many large enough to see without magnification, are water fleas (Branchiopoda-Cladocera), copepods (Copepoda), and seed shrimp (Ostracoda).

Amphibians and many insect species also live in vernal pools. The Pacific tree frog (*Hyla (Pseudacris) regilla*) and western toad (*Bufo boreas*) are common and abundant in and around vernal pools. Two rarer amphibians native to vernal pools are the California tiger salamander (*Ambystoma californiense*) and the western spadefoot toad (*Scaphiopus (Spea) hammondi*) (Morey 1998). While dispersing bullfrogs (*Rana catesbeiana*), which are not native to California, are sometimes found in vernal pools, they do not successfully breed there because bullfrog tadpoles require 2 years to mature and cannot survive the dry season. These voracious introduced predators will sometimes be found resting and feeding in vernal pools close to more permanent water, frequently associated with human modifications of the landscape. Fish likewise do not inhabit vernal pools, except where temporarily introduced by humans (e.g., mosquitofish (*Gambusia* sp.)) or by flooding of permanent waters.

The insect fauna of vernal pools is numerous, varied, and primarily native, including aquatic beetles (Coleoptera-Dytiscidae, Hydrophilidae, Gyrinidae, Halipidae, Hydraenidae); aquatic bugs, including backswimmers (Hemiptera-Notonectidae), water boatmen (Corixidae), water striders (Gerridae), springtails (Collembola), mayflies (Ephemeroptera), dragonflies, and damselflies (Odonata); and various flies with aquatic larvae, including midges (Diptera-Chironomidae), crane flies (Tipulidae) and mosquitoes (Culicidae). Rogers (1998) found that mosquitoes made up less than 2 percent of the total macroscopic invertebrate population in natural and 2-year-old constructed pools, perhaps because many of the other insects listed above are predators. Vernal pool crustaceans are an important food source for a number of aquatic and terrestrial species. Aquatic predators include insects such as backswimmers (Family Notonectidae) (Woodward and Kiesecker 1994), predaceous diving beetles and their larvae (Family Dystictidae), and dragonflies and damselfly larvae (Order Odonate). Vernal pool tadpole shrimp

are another significant predator of fairy shrimp (*Branchinecta* spp.).

The plants, invertebrate and vertebrate animals of vernal pools, and vernal pool landscapes in general are important providers of food and habitat for waterfowl, shorebirds, wading birds, toads, frogs, and salamanders (Proctor *et al.* 1967; Krapu 1974; Swanson 1974; Morin 1987; Simovich *et al.* 1991; Silveira 1996). During the spring, waterfowl feed on vernal pool crustaceans and other invertebrates, which are sources of protein and calcium needed for migration and egg-laying (Proctor *et al.* 1967; Silveira 1998). Vernal pool complexes contribute to continuity of wetland habitats along the Pacific Flyway (a major bird migration route). Many species feed or nest near vernal pools; for example, cliff swallows (*Hirundo fulva*) glean mud from vernal pool beds for their nests, lesser nighthawks (*Chordeiles acutipennis*) nest in dry vernal pool beds, burrowing owl (*Athene cunicularia*) and gopher (*Thomomys* spp.) burrows are found in mima mounds, and many species graze or hunt along vernal pool shorelines. Before their populations were nearly eliminated by hunting and habitat alteration, elk (*Cervus* spp.) and pronghorn antelope (*Antilocarpa americana*) undoubtedly grazed vernal pool landscapes, and have been replaced by cattle. There is additionally evidence that Native Americans in California's Central Valley used vernal pool crustaceans as a food source (Silveira 1998). Fishing net weights found near vernal pools suggest that California's first human populations also made use of vernal pool resources, as do hunters today (Silveira 1998).

Classification of Vernal Pools

The variability of vernal pool types has led many researchers to try and classify these ephemeral habitats. (Holland 1986; Sawyer and Keeler-Wolf 1995; Ferren *et al.* 1996; Smith and Verrill 1998). Most of these efforts have focused on classifying vernal pools based on the factors that influence variation in their physical features. Primary physical features that influence vernal pool size, depth, and soil and water chemistry include soil type, geologic formation, and landform. Landforms are physical attributes of the landscape resulting from geomorphological processes such as erosion and deposition, and include features such as alluvial terraces and basins and volcanic mudflows and lava flows.

The types and kinds of species that are found in vernal pools are largely