

determined by these physical factors (Holland and Griggs 1976; Zedler 1987; Eng *et al.* 1990; Holland and Dains 1990; Simovich 1998). The physical characteristics of the vernal pool influence the life history characteristics of vernal pool species, such as the speed with which a species can mature and reproduce, the amount of soil moisture required for germination of plant seeds or hatching of invertebrate eggs or cysts, as well as tolerance to turbidity, total dissolved solids, and other aspects of vernal pool water chemistry.

Sawyer and Keeler-Wolf (1995) classified vernal pools according to a number of physical, geographic, and biological characteristics. They identified several general vernal pool types, each of which corresponds to the nature of the impermeable layer that underlies the particular vernal pool and assisted that pool to form. The vernal pool types were identified as Northern Hardpan, Northern Claypan, Northern Basalt Flow, Northern Volcanic Mudflow, and Northern Ashflow vernal pools. Northern Hardpan vernal pools are formed on alluvial terraces with silicate-cement soil layers. These pool types are on acidic soils and exhibit well-developed mima mound topography found on the eastern margins of the Central Valley. Northern Claypan vernal pools are formed on impermeable surfaces created by an accumulation of clay particles. These pool types are often found on basin and basin rim landforms and tend to occur in the central portion of the Central Valley and tend to be alkaline. Vernal pools identified as Northern Volcanic Mudflow, Northern Basalt Flow, and Northern Volcanic Ashflow are formed by an impervious bedrock layer of volcanic origin. These pool types are found on the eastern and coastal portions of the Central Valley, and tend to be small and restricted in distribution. Northern Basalt Flow vernal pools occur at greater elevations than other vernal pool types.

The vernal pools in Southern California are associated with several soil series types including but not limited to Huerfueño, Olivenhain, Placentia, Redding, and Stockpen (Bauder and McMillan 1998). These soil types and other similar soil series like other vernal pool bearing soils and geologic formations have a nearly impermeable surface or subsurface soil layer with a flat or gently sloping topography (Service 1998). Due to local topography and geology, the pools are usually clustered into pool complexes (Bauder 1986; Holland and Jain 1988). Pools within a complex are typically separated by distances on the order of

meters, and may form dense, interconnected mosaics of small pools or a more sparse scattering of larger pools. The pools within the Santa Rosa Plateau in Riverside County, California are the only known locality for the Southern Basalt Flow Vernal Pools. Other vernal pools and pool complexes within the region, such as those at Skunk Hollow are not currently classified, but some of these pools converge on vernal lakes and others are associated with vernal alkali plains (Keeler-Wolf *et al.* 1998).

The vernal pools in the Agate Desert in Southern Oregon are located on alluvial fans capped with a shallow layer of clay loam over cemented hardpan. Other vernal pools within the area include those formed on older basaltic andesite formations such as those found on Table Rock. The vernal pool complexes are characterized by patterned ground with mounds and vernal pools. These pools vary in size from 1 to 30 m (3 to 100 ft) across, and attain a maximum depth of about 30 cm (12 in) (ONHP 1998). This landform is not true desert as it receives 48 cm (19 in) of precipitation annually. The pools within the area support the vernal pool fairy shrimp and other listed vernal pool species such as the endangered Cook's lomatium (*Lomatium cookii*) and large-flowered woolly meadowfoam (*Limnanthes floccosa* ssp. *grandiflora*) (Service 2002).

Vernal Pool Crustacean Background

All of the vernal pool crustacean species addressed in this critical habitat designation have evolved unique physical adaptations to survive in vernal pools. The timing and duration of wet and dry phases can vary significantly from year to year, and in some years, vernal pools may not inundate at all. In order to take advantage of the short inundation phase, vernal pool crustaceans have evolved short reproduction times and high reproductive rates. Most of the crustacean species addressed in this rule hatch within a few days after their habitats fill with water, and can start reproducing within a few weeks (Eng *et al.* 1990; Helm 1998; Eriksen and Belk 1999). Vernal pool crustaceans can complete their entire life cycle in a single season, and some species may complete several life cycles. Vernal pool crustaceans can also produce thousands of viable cysts when environmental conditions are favorable.

To survive the prolonged heat and desiccation of the vernal pool dry phase, vernal pool crustaceans have developed a dormant stage. After vernal pool crustacean eggs are fertilized in the

female's brood pouch, the embryos develop a thick, usually multilayered shell. When embryonic development reaches a late stage, further maturation stops, metabolism is drastically slowed, and the egg, now referred to as a cyst, enters a dormant state called diapause. The cyst is then either dropped to the pool bottom or remains in the brood sac until the female dies and sinks. Once the cyst is desiccated, it can withstand temperatures near boiling (Carlisle 1968), fire (Wells *et al.* 1997), freezing, and anoxic (deprived of oxygen) conditions without damage to the embryo. The cyst wall cannot be affected by digestive enzymes, and can be transported in the digestive tracts of animals without harm (Horne 1967). Most fairy shrimp cysts can remain viable in the soil for a decade or longer (Belk 1998).

Although the exact signals that cause crustacean cysts to hatch are unknown, factors such as soil moisture, temperature, light, oxygen, and osmotic pressure may trigger the embryo's emergence from the cyst (Brendonck 1996). Because the cyst contains a well-developed embryo, the animal can quickly develop into a fully mature adult. This allows vernal pool crustaceans to reproduce before the vernal pool enters the dry phase, sometimes within only a few weeks (Helm 1998; Eriksen and Belk 1999). In some species (e.g., vernal pool tadpole shrimp), cysts may hatch immediately without going through a dormant stage, if they are deposited while the vernal pool still contains water. These cysts are referred to as quiescent, and their presence allows the vernal pool crustacean to produce multiple generations in a single wet season as long as their habitat remains inundated.

Another important adaptation of vernal pool crustaceans to the unpredictable conditions of vernal pools is the fact that not all of the dormant cysts hatch in every season. Simovich and Hathaway (1997) found that only 6 percent of San Diego fairy shrimp (*Branchinecta sandiegonensis*) cysts hatched after initial hydration, and only 0.18 percent of Riverside fairy shrimp (*Streptocephalus woottoni*) cysts hatched. The cysts that do not hatch remain dormant and viable in the soil. These cysts may hatch in a subsequent year and form a cyst bank much like the seed bank of annual plants. Based on a review of other studies (Belk 1977; Gallagher 1996; Brendonck 1996), Simovich and Hathaway (1997) concluded that species inhabiting more unpredictable environments, such as smaller or shorter lived pools, are more likely to have a smaller percent of their