WETLANDS, Vol. 23, No. 3, September 2003, pp. 597–607

VERNAL POOLS AND THE CONCEPT OF ''ISOLATED WETLANDS''

Paul H. Zedler
Nelson Institute for Environmental Studies
and University of Wisconsin Arboretum
University of Wisconsin—Madison
Madison, Wisconsin, USA 53706

Abstract: Vernal pools, broadly defined as ephemeral wetlands that predictably form in permanent basins during the cooler part of the year but which dry during the summer months, are distributed throughout the world. In the U. S., they are particularly abundant on the Pacific Coast and in various forms in the glaciated landscapes of the north and northeast. Vernal pools are ecosystems that have evolved in a balance between isolation and connectedness. Because of isolation at several scales, the vernal pools biota includes many regionally endemic species. Because of connectedness, vernal pools also share many taxa with continent-spanning distributions at the generic and species level. Vernal pools serve an important local biodiversity function because of their connection to surrounding terrestrial habitats. Along with other ephemeral wetlands, they are the primary habitat for animal species that require relatively predator-free pools for feeding or breeding, including many amphibians. The recent U. S. Supreme Court decision (SWANCC), which deemed ''isolated'' wetlands to be outside the class of ''waters of the United States,'' places some significant but unknown proportion of vernal pools at risk. In the worst case, the consequences could be immediate reductions in biodiversity at a local level, and regional reductions over longer periods of time. Ideally, federal law should be rewritten to establish unambiguously the value of ephemeral wetlands. It will also be necessary for conservationists to educate the public and to bring the issue of vernal pool protection to the notice of their local and state governments.

Key Words: vernal pool, ephemeral wetland, isolated wetland

INTRODUCTION

The connectedness issue has always interested students of ephemeral wetlands, but it has assumed a new urgency with the recent Supreme Court decision to limit the Federal jurisdiction over so-called ''isolated wetlands'' (Solid Waste Agency of Northern Cook County v. U. S. Army Corps of Engineers, No. 99–1178—commonly referred to as ''SWANCC''). In this paper I review the ecological issues that have relevance to the question of how connected these distinctive habitats are to each other and to other ecosystems. The fact that views about degrees of connection have been brought into the legal arena also requires attention to the fine points of definitions that, in a purely scientific context, might not be a priority for discussion. If a habitat fits the definition of one that is legally protected, then it must be avoided or there must be mitigation. If it does not, the bulldozers can roll. It is therefore appropriate to begin by discussing the definition of vernal pool. I then consider these questions. 1) What is the nature of the connectivity of vernal pools to other vernal pools and other ecosystems? 2) How might the recent Supreme Court decision affect efforts to preserve vernal pools?

DEFINITIONS: VERNAL POOLS AND OTHER EPHEMERAL WETLANDS

As often happens, the ecological descriptor ''vernal pool'' was first used informally. It seems to have first appeared in the scientific literature in the 1920s, when W. L. Jepson and his students in California adopted it as one of a set of names for ephemerally wet depressions (Zedler 1987). The transition to a more precise usage began with Edith Purer's study of vernal pools of the San Diego region (Purer 1939). After regulatory protection was given to vernal pools by the Endangered Species Act of 1973, and by the U. S. Army Corps of Engineers and Environmental Protection Agency (1985 and 1988, respectively) under the Clean Water Act; the definition of vernal pool came to have legal implications in California, with a resulting tendency to apply the initially informal and casually defined name to the entire range of ephemeral wetlands deserving protection. At present in California, ''vernal pool'' has virtually driven out competing older terms, such as ''seasonally wet meadows,'' ''winter pools,'' and ''hogwallows.''

Working in the California context, Zedler (1987) took the narrow view, defining vernal pools as ephemeral wetlands of the Mediterranean climate region of the Pacific Coast, in broad agreement with other published treatments of vernal pools (e.g., Holland and Jain 1988). Habitats with the characteristics of vernal pools are not, however, restricted to Mediterranean climates. Keeley and Zedler (1998) gave a broader definition of vernal pools as ‘‘precipitation-filled seasonal wetlands inundated during a period when temperature is sufficient for plant growth, followed by a brief waterlogged terrestrial stage and culminating in extreme desiccating soil conditions of extended duration.’’ This definition includes habitats of non-Mediterranean climates, for example, the rock pools of eastern Georgia, U. S. It places vernal pools within the class of wetlands that Novitzki (1982) defined as ‘‘surface water depression wetlands.’’

A survey of the literature shows, however, that ‘‘vernal pool’’ is used much more broadly than even the definition of Keeley and Zedler (1998) would allow. For example, a search in Biological Abstracts from 1969 to mid-2002 on ‘‘vernal pool’’ turned up 66 abstracts for which it was possible to determine the region of the study. As expected, the majority (48) had reference to California, Baja California, or the Pacific Northwest, so that the Pacific Coast accounted for 73% of the citations. Other areas represented, however, were the northeast U. S. (6), the midwestern U. S. (3), Ontario, Canada (2), South and Central America (3), northern Europe (2), and southern Europe (2). The name has also been adopted by state resource agencies in the eastern U. S (e.g., Donahue 1996). Thus, ‘‘vernal pool,’’ whether by transfer or by independent invention is now applied to small wetlands that are present primarily or exclusively in the early part of the growing season and that typically ‘‘dry’’ completely or ‘‘substantially’’ at some point during the growing season. ‘‘Dry’’ is, however, quite variable within the broad definition. The vernal pools of Keeley and Zedler (1998) desiccate to a desertic extreme. The vernal pools of Massachusetts or Wisconsin, on the other hand, may support a lush herbaceous growth in the ‘‘dry’’ season. In Maine, the concept of vernal pool includes forested wetlands that are not distinguishable from other wetland types on the basis of vegetation (Calhoun et al. 2003 and A. Calhoun, pers. comm. 2003). To encompass this variation, vernal pools may be broadly defined as a subset of ephemeral wetlands that are generally small, form reliably (excepting perhaps the driest years) in a permanent basin (thus excluding more dynamic riparian-associated pools and disturbance-related road ruts), and which also dry reliably so that a large portion of the basin has a level of moisture at least as dry as that of the surrounding uplands. This definition includes pools that are in Novitzki’s (1982) class: ‘‘ground water depression wetlands,’’ but only if these have a high probability ($>$ 90%?) of being dry for a prolonged period during the growing season. Although at least some vernal pools of the northeast U. S. are known to be ground-water depression wetlands (e.g., in Maine, A. Calhoun, pers. comm. 2003) it is not clear what proportion are of this type (Golet et al. 1993, Brooks and Hayashi 2002). I believe that ‘‘vernal pool’’ should not include habitats that regularly remain wet enough through the growing season to be classified as swamp, marsh, fen, or another permanent wetland type. When not qualified in this article, vernal pool will be used in the moderately broad and somewhat fuzzy sense defined here.

By any definition, there is no sharp demarcation between vernal pools and other ephemeral wetlands. For example, at least some ‘‘prairie potholes’’ or ‘‘Carolina bays,’’ if they held water primarily early in the year, could qualify as vernal pools. Such overlap is to be expected when a definition has grown organically. What is important is to recognize the diversity of ephemeral wetlands, and to understand how size, landscape position, hydrology, and other factors, including degree of isolation at different spatial and temporal scales affect their structure and function. Our choice of names should be designed to ensure that no ephemeral wetland is left behind when we design conservation programs.

Some peculiarities of terminology deserve mention. One arises when ‘‘vernal pool’’ is used to classify a specific habitat patch. In fact, vernal ‘‘pools’’ are really a sequence of habitats. In California, for example, one can identify four phases (Zedler 1987): 1) a summer desert-like dry state, 2) a pre-inundation wetting phase as germination and hatching are stimulated by the first rains, 3) a pool phase, and 4) a drying phase as the water evaporates and seeps away and the exposed substrate begins to dry. For most of the year there is discordance between the name and the observable state. Someone taken to view a vernal pool in late summer sees not a pond but a desiccated basin. The expert can accept the poolness of this habitat, but the obvious discrepancy could be ammunition for the unscrupulous who wish to make a mockery of preserving ‘‘dried up puddles.’’ Another difficulty arises with vernal pools of more humid regions. Some of these fill not only in the spring but also in the fall, when cooler temperatures and rainfall can create an autumnal phase of a ‘‘vernal’’ pool (Anonymous 2001).

The Uniqueness of Vernal Pool Ephemeral Wetland Habitat

As noted, the uninformed can view vernal pools as insignificant marginal habitats—failed ponds or upland areas with an easily rectified seasonal drainage prob-

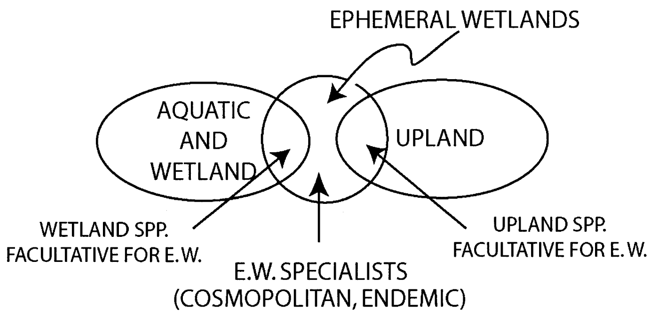

Figure 1. On the assumption that upland and wetland habitats do not overlap, ephemeral wetlands can be viewed as transitional between them. The location and nature of ephemeral wetlands is highly varied. In this paper, the focus is on vernal pools, broadly defined. This includes wetlands that dry each year for extended periods, as well as those that may only dry completely in extreme years. The biota of ephemeral wetlands is a mixture of ephemeral wetland specialists plus species from wetland and upland habitats that tolerate fluctuating or temporary water but have their primary distribution outside of ephemeral wetlands.

lem (e.g., by ''deep ripping''; Lamb 2002). Scientific study has revealed, however, that temporary aquatic habitats are the primary or exclusive habitat for a rich array of highly specialized organisms. The quality that vernal pool specialists share is the capacity to deal with the dramatic changes in the local hydrological regime and to exploit these changes to their benefit. For these plants and animals, the vernal pools are not marginal, but essential (Fig 1).

A key feature of vernal pools of all types is that they are landscape features as permanent as rivers, lakes, and marshes. The ponded water comes and goes during the year, but it is present for at least a short time in most or all years. It is the predictability of reappearance that allows a distinctive biota to develop.

VERNAL POOL HYDROLOGY

The more-or-less reliable presence of standing water of limited duration is the defining feature of vernal pools. The requirements for ponding are the presence of a basin and inputs of water that exceed losses for part, but not all, of the year. Since vernal pools are lentic, basins that are ponded but have continuous outflow because of inputs from surface flow or ground water are not considered vernal pools. Matters are less clear, however, with respect to the contribution from subsurface inflows. Keeley and Zedler (1998) emphasized that vernal pools are rain-fed systems in which the basins pond because of the collection of direct precipitation and some runoff at rates that exceed losses. As noted above, a definition broad enough to encompass vernal pools of the northeastern U. S. admits some pools for which the permanent ground-water table plays a role. Of course, ''ground water'' of some sort is a factor in any vernal pool except perhaps those in completely impervious rock basins. The main question is if the ground water is a net source or sink for water in the pool. In California, the vernal pools mostly have ''top-down'' hydrology, with water collecting in the basins and creating a locally perched water table above a soil horizon of very low hydraulic conductivity (Zedler 1987, Hanes and Stromberg 1998). In these pools, the perched water table develops because of infiltration from the basins, although at particular times during the filling and drying phases, the direction of flow can be in either direction. In more humid regions, some pools are of this type, but others may have connections to the permanent ground water (Brooks and Hayashi 2002). Some of these may be of the ''bottom up'' variety, where pools are created by the seasonal rise of the water table. A problem is that perched and permanent ground-water bodies can merge in various ways that might defy simple classification (e.g., Salve and Tokunaga 2002). The common element of vernal pool hydrological regime is that it is sensitive to seasonal input-output relations. In the Mediterranean climates of California, the winter rains provide a strong seasonal pulse. In the Northeast, it seems to be the initially high soil moisture associated with snowmelt plus early spring rains that are important (Schneider and Frost 1996). In both systems, the coincidence of the precipitation-related input with reduced winter and early spring temperatures and shorter day length and therefore reduced evapotranspiration contribute to the seasonal presence of standing water.

Vernal pools are therefore at the upper end of the water-distribution network. They are collectors of rainfall and melt water. Although it is common for them to overflow into regional drainages, in all cases, a significant proportion of the water collected in the basin is lost to seepage and evapotranspiration, the relative importance of these two losses being a function of the basin soils and geological substrate, the climate, and the density and type of vegetation supported.

VERNAL POOLS AS ECOLOGICAL REFUGES

For animal species that depend on the presence of standing water, a critical feature of vernal pools is that they have reduced predator populations. The short duration of the standing water and the general lack of inflow connection to regional wetlands creates a refuge from the larger predators of more permanent waters (Williams 1987, Wellborn et al. 1996). Fish cannot persist in ponds of short duration (in general, but see Berra and Allen (1991) for an Australian exception), and other vertebrates capable of dispersing overland or in the air cannot find dispersed habitats fast enough to exert continuous predation pressure. Some predaceous beetles and hemipterans are an exception to this pattern, since they have a remarkable facility for locating small ponds (Roth and Jackson 1987, Williams 1987). Overall, however, studies have confirmed that the impact of predators increases with the duration of the ponding (e.g., Schneider and Frost 1996, Wellborn et al. 1996, Bilton et al. 2001). The reduced predation pressure of ephemeral wetlands opens the habitat for vertebrate pond-requiring species that are vulnerable to predation and allows behaviors that would put them at risk in permanent ponds (Skelly 1996, Boix et al. 2001). The same explanation applies to smaller animals such as fairy shrimp (Anostraca, Crustacea), one of the notable and widely distributed groups of ephemeral wetland specialists (Williams 1987). These quintessential ephemeral wetland aquatic invertebrates swim at a leisurely pace in open water, so that they are easily taken by fast moving predators, as some experimental studies have shown (Schneider and Frost 1996). Whereas ephemeral wetlands provide predator-reduced habitats, they also present a challenge—high habitat variability. There is the risk that the habitat will dry before the species can complete the aquatic phase of its life cycle and then the problem of surviving through the drought to the next episode of pool filling. The pool specialists have evolved a capacity to respond quickly to pool formation, reach reproductive size in a short period, and persist in (many invertebrates) or near (most amphibians) the pools through the drought.

Given the broad and somewhat imprecise definition of vernal pools, it is not surprising that pools differ markedly in hydroperiod (duration of standing water) and other aspects of hydrology (depth of water, frequency of dry-down, persistence of saturation at the surface, etc.). These differences matter to the specialist fauna. A given vernal pool will typically be suitable habitat for only some species. In Rhode Island, for example, optimal hydroperiods for amphibians, as estimated by survival to metamorphosis, ranged from 125 to over 580 days (Paton and Crouch 2002). Some of the rare invertebrates, such as fairy shrimp, do better with shorter durations, presumably because their smaller size makes predator-susceptibility a factor earlier in the season. These patterns mean that preservation of regional species diversity requires attention to ephemeral wetland diversity.

For the vernal pool vascular plants, the advantage of the ephemeral habitat has more to do with competition than predation. The presence of standing water excludes or limits the growth of plants of the surrounding uplands, but likewise, the ultimate drying of the habitat excludes or limits species of permanent marshes. Thus, a window of opportunity is presented for plants that can tolerate the extreme alternation of wet and dry. As for animals, the ephemeral habitats have been the cradle of highly specialized plant taxa with a long evolutionary history. This is evidenced by sets of correlated traits, such as a capacity for persistence of the seeds in the soil, limited capacity for dispersal, and plastic growth forms that accommodate the transition from aquatic to terrestrial existence (Zedler 1990). For most species, this history extends at least a million or more years into the past. Others, such as the remarkable genus *Isoetes* (quillworts), are even more ancient specialists (Pigg 1992). These small, grass-like plants are found worldwide, and paleobotanical data suggest that they were present as aquatic specialists some time prior to the breakup of Gondwanaland about 140 million years ago (Taylor and Hickey 1992). At present, some of the 150 *Isoetes* species are wholly aquatic and others completely terrestrial, but most occur in habitats with fluctuating water levels. Of eight species in northeastern North America, for example, four are found in amphibious habitats, one in fluctuating or permanent water, two are generally permanently submersed, and one is wholly terrestrial (Gleason and Cronquist 1991). The genus is also notable for possessing Crassulacean acid metabolism (CAM), which until it was discovered in *Isoetes howellii* Engelm. in a California vernal pool, was a physiological mechanism that was thought to be confined to terrestrial plants, especially those of arid regions (Keeley 1996). CAM provides *Isoetes* with the capacity to optimize its uptake of CO_2 by storing it during the night and using it to photosynthesize during the day (Keeley 1996). Thus, *Isoetes* is both very ancient and highly specialized. This is powerful evidence for the continuity of ephemeral wetland habitats over immense periods of time.

THE CONNECTEDNESS ISSUE

The Global Distribution of Ephemeral Wetland Taxa

If a species evolves a life history that enables it to exploit the ecological opportunity offered by vernal pools, and if ''vernalpoolness'' is a recurring pattern, it would be expected that such specialists would spread from their place of origin. This process presumably got its start at the earliest stages of the invasion of the land, when some of the organisms that expanded into freshwaters developed the key traits that allowed them to invade ephemeral ponds wherever they occurred. This seems to be the explanation for the worldwide distribution of ephemeral wetland groups such as the Anostracans, Conchostracans, and plant groups like the aquatic ferns *Marsilea* and *Pilularia* and the *Isoetes* discussed above.

The animals, most notably the crustaceans, are evidence of connections that extend across time as well as across space. *Branchinecta*, an Anostracan (fairy shrimp) genus, for example, is found on every ice-free continent but Australia; another genus, *Streptocephalus*, is found throughout the northern hemisphere and in Africa (Belk 1996). In the 48 states of the continental U.S., a recent compilation shows that seven of the total of 14 species of *Streptocephalus* are regional endemics limited to one or a few states, whereas the genus as a whole occurs in 18 states, with no doubt more occurrences to be discovered (Jass and Klausmeier 2000). The genus *Eubranchipus* has nine species in the U. S., two of which are regional endemics, while the genus collectively occurs in 36 of the 48 states from the east to the west coasts (Jass and Klausmeier 2000). There is reason to believe that the vast spatial range is matched by a long history. This is certainly the case for another group of ephemeral wetlands specialists, the conchostracans (clam shrimp). Tasch's study of fossil clam shrimp showed that regionally distinct assemblages were present across Gondwanaland in the Paleozoic (Tasch 1987).

It is of special importance to the conservation of biodiversity to realize that the degree of local specialization and endemism in these widespread groups is only beginning to be understood, with many new species coming to light in recent years (e.g., Fugate 1993).

The Disconnectedness Issue: Vernal Pool Isolation Stimulates the Evolution of Endemic Species

The tendency for widespread genera to spin off local endemics is evidence that the connectedness demonstrated by the existence of a world-wide specialist biota is countered by a degree of isolation sufficient to allow regional selective forces to act. In some cases, these forces have produced assemblages that include many of the widespread groups but that also contain unique endemic genera and species. The repeating pattern of endemic species in a number of genera is strong evidence that these endemics evolved within the region. This phenomenon is best reported for the vernal pools of California, but it also a feature of vernal pool habitats in other regions. This can be illustrated by considering some of the most species-rich plant genera of California vernal pools (Table 1). Note that with the exception of the genera *Eryngium*, *Eleocharis*, and *Juncus*, these consist mostly of annual species. This can be explained by the fact that vernal pools favor species that are able to tolerate highly variable timing for the onset and duration of the growing season and also endure long periods of extreme dryness. Surviving as a seed is one of the best means of dealing with extreme conditions (Baskin and Baskin 1998). Larger perennials that become dominant in more permanent habitats by vegetative spread, such as *Typha* spp. and *Scirpus* spp., are excluded completely from vernal pools or limited to only the deepest areas of longest water duration. This opens the habitat for the annuals (Zedler 1990).

Table 1. Taxa-rich vascular plant genera of California vernal pools. Data from Keeler-Wolf et al. (1998). Because of nomenclatural problems, the exact number of distinct taxa is a matter of dispute. Here I use only species. Many of these species show strong geographical patterns of sub-specific variation. Those with a double asterisk are genera endemic to or primarily associated with the California Floristic Province (Raven and Axelrod 1978; Hickman 1993). Genera with a single asterisk contain at least one endemic species. *Orcuttia*/*Tuctoria*/*Neostaphia* is a group of closely related genera of uncertain taxonomic affinity sometimes segregated as the tribe Orcuttieae. Data on endemism from Raven and Axelrod (1978).

Genus	Family	Number of Spp.	Number of Annuals
*Navarretia**	Polemoniaceae	7	7
*Downingia***	Campanulaceae	13	13
*Juncus**	Juncaceae	13	7
*Limnanthes***	Limnanthaceae	7	7
*Plagiobothrys**	Boraginaceae	15	14
*Eryngium**	Apiaceae	10	0
*Lasthenia***	Asteraceae	9	9
Psilocarphus	Asteraceae	4	4
*Orcuttia***/*Tuctoria***/*Neostaphia***	Poaceae	7	7
Eleocharis	Cyperaceae	5	1
*Pogogyne***	Lamiaceae	6	6
Elatine	Elatinaceae	5	5

In a seeming contradiction, the drying out and the shift to a Mediterranean-type winter rainfall pattern that occurred in the western U. S. beginning in the early Tertiary (Axelrod 1988) provided an opportunity for an ephemeral wetland biota to flourish. Permanently wet places presumably became seasonally wet, and depressions that were shaded by trees were opened to full sun. Also during the Tertiary, the Central Valley (Great Valley) emerged to provide a vast mostly level or gently sloping landscape as exemplified by the Oligocene and Miocene deposits described by Bartow (2000). The result was a radiation of suitably adapted plant genera, which spun off locally adapted species across the region as the ephemerally wet habitats proliferated. The species of the Limnanthaceae provide a clear example. This family contains two genera. *Floerkea* has only one species, *F. proserpinacoides* Willd., a small-flowered annual that has a broad geographic distribution in seasonally moist or inundated rich deciduous forests of the eastern U. S. and wet places in forests or shrublands of the west. It is usually regionally rare but abundant where it is found. The eponymous genus, *Limnanthes*, consists of about nine annual species that are limited to the Pacific west (Hickman 1993). Most of these are amphibious outcrossing species with relatively large, showy flowers. They germinate early in the season and tolerate standing water but flower mostly as the pools dry, usually in colorful masses. It seems reasonably certain that *Limnanthes* derived from one or a small number of species with *Floerkea*-like ecology whose populations expanded as increasing dryness sharpened the contrast between wet and dry seasons and large areas of habitat with fluctuating hydrology became available. Spencer and Porter's (1997) study of relationships in the genus *Navarretia* (Polemoniaceae) using nuclear ribosomal DNA reveals another pattern. They found that this predominantly upland and dry habitat genus of annuals has one clade of ephemeral wetland specialists that radiated relatively recently from a single taxon. Radiation and geographic speciation in vernal pools are found in the other genera listed in Table 1.

Vernal pools in California also support species from a generalized ephemeral wetland biota that are widely distributed. Examples of plants in this category are *Lilaea scilloides* (Poiret) Hauman (found throughout a wide area of the west and in South America) and *Crassula aquatica* (L.) Schönl. a diminutive species found in the eastern U.S. and Eurasia, as well as the pools of California.

The significance of these facts to the question of isolation is that vernal pools of California have both a strong connectedness by a sharing of common elements and a distinctiveness that is attributable to their relative isolation. The present biota is a result of these countervailing tendencies.

Vernal Pools and the Isolation-Exchange Balance

Holland and Jain (1981) demonstrated the utility of viewing vernal pools as islands, which by definition emphasizes isolation. They and Keeler-Wolf et al. (1998), however, also stressed the hierarchical nature of the isolation, with pools clustered to form ''archipelago-like'' groupings within which exchange could be frequent and therefore of ecological and evolutionary importance. This view is reinforced by a recent study that demonstrated a ''genetic rescue'' phenomenon in rock pools (Ebert et al. 2002) in which local interpool dispersal was shown to be a potentially potent force counteracting the disadvantages of inbreeding in small populations. These studies also support the concept that it is a balance of isolation and exchange that must be invoked to understand the ecology and evolution in vernal pools and that local exchange and metapopulation dynamics may be important in some systems of isolated wetlands.

Study of invertebrates in ponds and ephemeral wetlands (e.g., King et al. 1996) has provided further insights, demonstrating a degree of endemism indicative of vicariant speciation within widely dispersed groups comparable to that of the plants (e.g., Taylor and Hickey 1992). The patterns they reveal could not occur unless the groups of vernal pools were relatively isolated in ecological time but connected in evolutionary time. Studies of dispersal among aquatic habitats gives somewhat contradictory results showing both ready dispersal of some species (e.g., Proctor and Malone 1965, Figuerola and Green 2002) but also instances where dispersal even over short distances seems to be very low (Bilton et al. 2001, Caceres and Soluk 2002).

Ecological connectedness at the meso-scale is also strongly implied by the present pattern of distribution of some species. *Howellia aquatilus* A. Gray, an endangered robust annual found in ephemeral habitats in the Pacific Northwest, has relatively small populations, limited seed production, and limited seed dormancy and seed longevity, which make the local populations susceptible to local extinction in dry periods (Lesica 1992). As a result, its populations fluctuate widely. It is therefore clear that the survival of the species in any area is dependent on its persistence in the larger and deeper ponds that form even in drier years. From these refuges, it is able to disperse out into smaller pools to reestablish populations lost during droughts (Lesica 1992). Although the species has not been followed long enough to confirm this, it is reasonable to hypothesize that, in a run of very wet years, the most favorable habitat for the species will be smaller, less persistent pools, thereby reversing the roles of pools as refugia. Such metapopulation processes almost certainly exist in other species and groups and underscore the importance of inter-pool exchange and of maintaining a diversity of pool sizes within a region.

Surviving vernal pools, however, exist in very different landscapes from those in which they evolved. California provides an extreme example. In the original landscape, vernal pools were widely distributed but were only one element of a regional wetland complex, with the vast marshes and shallow fluctuating lakes of the Central Valley at its core. All of the endemic genera of California vernal pool plants occur in the Central Valley, and it is reasonably certain that the Central Valley was the focal region in which the late Tertiary and Pleistocene radiation and local specialization took place. The more remote regions very likely were the recipients of taxa dispersing outward from this core area. Starting in the early 19th century, however, the Central Valley system of wetlands was first severely disrupted and then mostly destroyed. As an example, Lake Tulare, once a marshy lake over 35 km long and 25 km wide, has been reduced to a tiny sump in semi-desert surroundings by diversion of the inflows and the pumping of ground water for irrigation (Preston 1981). Similar destruction of wetland habitat occurred throughout the valley, including the leveling of vernal pool-supporting Mima mound topography for agriculture (Nikiforoff 1941). It is estimated that less than 10% of the original area of wetland remains in California, and much of what survives is drastically altered from its natural state, with low biodiversity value. These massive alterations have completely reworked the patterns of exchange among the remaining vernal pools. To cite the most obvious example, the numbers of migrating waterfowl are a fraction of what they were prior to agricultural development, and the migration routes are different. Since waterfowl are known to be dispersers of aquatic organisms and plants (e.g., Taylor and Hickey 1992), it follows that the numbers and kinds of plant propagules being moved across the landscape must also have been altered significantly. The process of relaxation (the loss of species to extinction because of reduced population size), compounded with the problem of invasion, suggests that the remaining isolated vernal pool habitats will tend to lose species diversity over time as the proportion of endemic native species dispersed falls relative to that of weedy natives and exotics. The process could be insidious because it may happen so gradually that it may not be detectable by existing monitoring methods until the vernal pool system enters a new domain inimical to the survival of the most valued elements of the vernal pool biota.

Inter-Continental Exchange as Evidence of Connectedness

Connectedness can exist even over continental distances. A number of genera in western North America have one or a small number of species that appear in temperate South America, with no known populations in either the tropical lowlands or montane environments in between (Raven 1963, Zedler 1987). Many of these genera are ephemeral wetland plants. These so-called ‘‘amphitropical disjuncts’’ are evidence that connections between ephemeral wetlands can exist over vast distances. For example, the genus *Downingia* consists of 13 species, all annual. One, *D. pusilla* (Don) Torrey, is found in both California and in the vernal pools of Chile (Bliss et al. 1998). Significantly, this species is one of two in the genus that appears to be predominantly self-pollinating. A recent phylogenetic analysis of the genus using several types of molecular data confirms that the South American *D. pusilla*, although distinguishable from the North American material, is very closely related to it. This confirms that the South American populations must have been established in Chile by dispersal from North America (Schultheis 2001). A similar situation holds for species pairs in *Lasthenia*, *Blennosperma*, and other genera (Bliss et al. 1998).

Hydrologic Connectedness

As noted above, vernal pools are at the upper end of drainage systems, and many never have surface connections to other aquatic systems. It does not follow, however, that they have no significant connections whatsoever. Undrained depressions tend to occur in more-or-less level topography, and many vernal pools are elements of a temporary drainage network in which the pools are storage basins connected during times of maximum rainfall. These networks can be endorheic in the strict sense, with no outflow to regional drainages, or they can spill into permanent streams or lakes. In all cases, there is the potential for the water in the storage basins to seep downward through the soil layers that create the perched water table. The significance of this seepage is that it can transfer water from surficial layers where it will be lost by evapotranspiration to ground water where it can feed permanent springs, seeps, creeks, or simply enhance the ground-water supply of riparian zones without reaching the surface. The surface/depth balance is illustrated by a study of Salve and Tokunaga (2002) of seepage in a semi-arid catchment in north-central California. In their situation, which lacked vernal pools, transfer to base flow occurred when saturated conditions reached a shallow soil/bedrock interface, whereas in the deeper soil areas many rainfall events served only to recharge the zone subject to loss through evapotranspiration. Pooling of water can produce a similar effect by creating a local patch of saturation that will permit either movement along the surface of the impermeable zone (if it is sloped) or mass flow to deeper layers through cracks in the impeding layer, as seems to occur in southern California vernal pools (Zedler 1987). Leveling the topography in a region of vernal pools therefore has the potential to cause a significant reduction in deep penetration of water. A study by Desconnets et al. (1997), in an area of the Sahel desert in which pools are common, shows this effect very clearly. They found that pooling made a significant contribution to the regional aquifer recharge. This effect is not limited to semi-arid regions. The construction of ‘‘rain-gardens’’ is being promoted in the humid upper Midwest for their value in aquifer recharge (K. Potter, University of Wisconsin- Madison, personal comm. 2003). The irony of an effort to create artificial ephemeral wetlands, even as natural ones are being destroyed, needs no emphasis.

The examples show clear evidence of hydrologic connectedness. Of course, the contribution of individual pools to this connectedness will vary. From a policy point of view, however, it is imprudent to disregard this potentially significant function, especially when its importance has only recently been appreciated.

Local Biodiversity Function of Vernal Pools

Vernal pools have a remarkably distinct biota, of which the regionally endemic vernal pool specialists are a notable feature. For these species, destruction of habitat threatens complete extinction. There are many other species of wider distribution, however, for which vernal pools are critically important habitat. Such species may not be in imminent threat of extinction globally, yet destruction of habitat may upset local foodwebs and cause local extinctions that result in the impoverishment of local biodiversity. A failure to regulate destruction of vernal pools may lead cumulatively to the loss of even presently widespread species (Semlitsch and Bodie 1998, Gibbons 2003). In many species of frogs and salamanders, adults seek out vernal pools early in the season and mate and lay eggs in shallow pools. The young develop in the pools and metamorphose to their terrestrial form, after which they disperse into non-aquatic habitats in the surrounding landscape where they feed and aestivate or hibernate (Kenney and Burne 2001, Gibbons 2003). As noted above, predator-free ponds appear to be critical. Many amphibians cannot successfully breed in permanent waters where the eggs and aquatic stages of the young are highly vulnerable. Elimination of ''unconnected'' wetlands could be devastating to amphibians (Semlitsch and Bodie 1998).

California vernal pools provide other examples. One is the suite of insects specialized to act as pollinators for some of the relatively large-flowered annuals of vernal pools (Thorp and Leong 1998). Vernal pools also play an important and under-appreciated role for many birds (Silveira 1998).

As noted by Calhoun et al. (2003) many of the vernal pool dependent species are equally dependent on the surrounding upland. Conservation of vernal pool fauna therefore requires a landscape perspective.

A ''SIGNIFICANT NEXUS''?

The information presented above supports the contention of Tiner et al. (2002) that isolation is a relative concept. If the criterion of isolation is ''unreachable from deepwater ports by commercial watercraft,'' every vernal pool this author is familiar with is isolated. With respect to reasonable and conservative biological and landscape measures, however, vernal pools are most definitely not isolated. The SWANCC decision has contributed to the confusion by introducing the concept of ''significant nexus'' as the test for whether or not wetlands are to be part of the waters of the United States. To the ecologist, vernal pools have a significant nexus with respect both to the surrounding uplands and to other aquatic habitats. The examples given above show interchanges at all temporal and spatial scales. Thus, from an ecological point of view, drawing a line at the limits of Federal concern for wetlands that places ephemeral wetlands like vernal pools on the ''not requiring attention'' side of the line is an affront to our understanding of ecological realities. Should this ecological point of view have any standing before the Supreme Court? One hopes that it would, because it would seem that the welfare of the biosphere is a proper matter for the attention of the federal government.

Consequences of SWANCC

It is too early to know exactly what the consequences of SWANCC will be for vernal pools (Kusler 2003). In the west, many pools continue to be afforded protection under the Endangered Species Act, which is administered by the U.S. Fish and Wildlife Service. This protection is only invoked, however, when proposed actions have some component of Federal involvement. This includes all federal actions, most state actions, and a significant proportion of private projects beyond the smallest and most local. In contrast, under Section 404 of the Clean Water Act, the U.S. Army Corps of Engineers has jurisdiction over all waters of the United States. Weakening the ability of the Corps to act in cases involving vernal pools is therefore of concern.

Many vernal pools discharge into adjacent riparian systems during periods of high rainfall, some annually, many more in years of exceptionally high rainfall. In this case, it can be argued that they are a part of the waters of the United States because of this direct connection. By definition, however, most vernal pools have such connections only for short periods. If SWANCC is a signal that the U. S. judiciary is looking for ways to remove the federal government from the regulation of wetlands wherever possible, then one must be concerned that such ephemeral connections will be discounted because of the relatively small volumes of water and the short duration of connections. Most vernal pool swales will not float a Mississippi River barge. That such brief and shallow connections play a critical role in biodiversity maintenance may fail to persuade the higher courts if they see issues like species extinction being of concern primarily to the states.

To develop solid estimates of just how much is at risk would require that one have in hand the results of careful delineations of vernal pools. Most existing databases fall far short of the ideal. In California, there is good information on general distribution (e.g., Holland 1998, Keeler-Wolf et al. 1998), but comprehensive data that would allow pools to be divided into potentially protected from unprotected are lacking. The situation appears to be even less satisfactory in the east, where general recognition of the value of vernal pools is a more recent development (Preisser et al. 2000). A determination of pools and pool habitat area at risk would require that vernal pools already in dedicated natural areas and reserves be subtracted from the total and that the characteristics of vernal pools on private lands or the few public lands on which development is a threat be known. Vernal pools on private lands are, however, those about which the least is known (e.g., Preisser et al. 2000).

Although it is very difficult to assign numbers, it is easy to see which types of vernal pools are most at risk. The probability of preservation decreases sharply with size, distance from the nearest regulated body of water (adjacency), the number of species of special concern, and the frequency and size of ephemeral connections to other habitat. Which of these negative correlates is most pronounced will vary by region. In the East, because of the greater abundance of regulated aquatic habitats, more vernal pools may be afforded protection on the basis of adjacency, but fewer will get protection because of endangered species. In the West, many vernal pools will be more isolated, but more will contain rare species. The vernal pools of extreme southern California have the dubious advantage of having gone through drastic reduction in extent, with the resulting ''benefit'' that endangerment is obvious without resort to complex population models. The impending loss of all pools therefore stimulated efforts to save the few remaining examples. As a result, little vernal pool habitat not already covered in concrete remains in private hands. The situation is different further north, where much vernal pool habitat is in private ownership and where, in some cases, few or no endangered species are present. What this geographic correlation with likely degree of wetland loss means is that some areas could suffer more pronounced loss of wetlands and greater local effect because, in some localities, vernal pools are a large portion of what remains of wetlands (Tiner et al. 2002).

However one looks at the situation, it seems clear that there are vernal pools now at risk that previously had protection under the Clean Water Act (Kusler 2003). The history of vernal pool destruction in California, for example, includes more than one instance in which some individuals were willing to take a chance by acting first and asking later, or not asking at all. Sometimes, these persons went too far and were successfully sued by the U.S. Environmental Protection Agency. At other times, those who aggressively ''pushed the envelope'' managed to circumvent the spirit of wetland and endangered species regulations and destroyed natural habitats without consequences. It is to be expected that some who are unsympathetic to conservation–based constraints will be prepared to force the issue on the chance that regulators will be unwilling to fight over wetlands that can be argued out of existence because they are ephemeral. A recent case in San Diego, in which pools supposedly dedicated for preservation were destroyed without consequences, may be a portent of things to come (McDonald 2002).

What Should be Done?

An effort needs to be made to convince Congress to revise the Clean Water Act to make it explicit that all wetland habitats, including ephemeral wetlands, deserve protection (Ruffolo 2002, Kusler 2003). It is also necessary to argue vigorously against using SWANCC to justify administrative actions to weaken wetlands protection. On the contrary, as Kusler (2003) points out, an effort should be made to convince the administration to promulgate policies that will cover the gaps exposed by SWANCC. It would be a mistake, however, to place all hopes on success at the federal level. Wetland scientists must also work within each state to promote regulations that protect the wetlands left at risk by SWANCC. The success of this approach in Wisconsin (Christie and Hausmann 2003) shows that the argument for wetland protection need not be a partisan issue. There is reason to be hopeful that similar efforts in other states will be successful. Another avenue for furthering regulatory reform is through organizations like the International Association of Fish and Wildlife Agencies, which has in the past served to coordinate conservation efforts nationally and internationally (G. Cintron, pers. comm. 2002).

Efforts should not be limited to strengthening regulation. A founding tenet of the United States is that a government rules by consent of the governed. This principle applies as well to wetland regulation. We must work to make our fellow citizens understand the functional and aesthetic values of wetland habitats and to build a consensus to counter the narrow views that seem to be emerging among decision makers in high places. Optimists (e.g., Adler 1999) assure us that appeals to good nature augmented by appropriate incentives are sufficient to guarantee that valuable habitats will be preserved. Many, however, will want at least a dash of regulation in the mix. We can all agree, however, that it is important to work creatively to inform the public about the value of ephemeral wetlands and to make our fellow citizens feel good about preserving this important element of the biosphere (Calhoun et al. 2003).

ACKNOWLEDGEMENTS

Tracie Nadeau and Scott Leibowitz suggested many changes and encouraged me to broaden the coverage of vernal pools. The manuscript benefited greatly from the comments of Gilberto Cintron-Molero and an anonymous reviewer.

LITERATURE CITED

Adler, J. H. 1999. Swamp rules: the end of Federal wetland regulation? Regulation 22:11–16.

Anonymous. 2001. Rhode Island vernal pools. Web site: http://www.uri.edu/cels/nrs/paton/vernal_pool_def.html

Axelrod, D. I. 1988. Outline history of California vegetation. p. 139–193. *In* M. G. Barbour and J. Major (eds.) Terrestrial vegetation of California, new expanded edition. California Native Plant Society, Sacramento, CA, USA.

Bartow, J. A. 2000. Tuffaceous ephemeral lake deposits on an alluvial plain, Middle Tertiary of central California. Sedimentology 41:215–232.

Baskin, C. C. and J. M. Baskin. 1998. Seeds. Ecology, biogeography, and evolution of dormancy and germination. Academic Press, San Diego, CA, USA.

Belk, D. 1996. Was sind ''Urzeitkrebse''? Stapfia 42:15–19.

Berra, T. M. and G. R. Allen. 1991. Population structure and development of *Lepidogalaxias salamandroides* (Pisces: Salmoniformes) from Western Australia. *Copeia* 1991:845–850.

Bilton, D. T., J. R. Freeland, and B. Okamura. 2001. Dispersal in freshwater invertebrates. Annual Review of Ecology and Systematics 32:159–81.

Bliss, S. A., P. H. Zedler, J. Keeley, and M. K. Arroyo. 1998. A floristic survey of the temporary wetlands in the mediterranean-climate region of Chile. p. 219–28. *In* A. J. McComb and J. A. Davis (eds.) Wetlands for the future. Proceedings of the INTECOL Conference on Wetlands. Perth, Australia. Gleneagles Publishing, Adelaide. Australia.

Boix, D., J. Sala, and R. Moreno-Amich. 2001. The faunal composition of Espolla pond (NE Iberian Peninsula): The neglected biodiversity of temporary waters. Wetlands 21:577–592

Brooks, R. T. and M. Hayashi. 2002. Depth-area-volume and hydroperiod relationships of ephemeral (vernal) forest pools in southern New England. Wetlands 22:247–255.

Caceres, C. E. and D. A. Soluk. 2002. Blowing in the wind: a field test of overland dispersal and colonization by aquatic invertebrates. Oecologia 131:402–408.

Calhoun, A. J. K., T. E. Walls, S. S. Stockwell, and M. McCollough. 2003. Evaluating vernal pools as a basis for conservation strategies: A Maine case study. Wetlands 23:70–81.

Christie, J. and S. H. Hausmann. 2003. Various state reactions to the SWANCC decision. Wetlands 23:653–662.

Desconnets, J. C., J. D. Taupin, T. Lebel, and C. Leduc. 1997. Hydrology of the HAPEX-Sahel Central Super Site: surface water drainage and aquifer recharge through the pool systems. Journal of Hydrology 188–189:155–178.

Donahue, D. F. 1996. A Guide to the Identification and Protection of Vernal Pool Wetlands of Connecticut. University of Connecticut Cooperative Extension Program. Storrs, CT, USA.

Ebert, D., C. Haag, M. Kirkpatrick, M. Riek, J. W. Hottinger, and V. I. Pajunen. 2002. A selective advantage to immigrant genes in a Daphnia metapopulation. Science 295:485–88.

Figuerola, J. and A. J. Green. 2002. Dispersal of aquatic organisms by waterbirds: a review of past research and priorities for future studies. Freshwater Biology 47:483–94.

Fugate, M. 1993. *Branchinecta sandiegoensis,* a new species of fairy shrimp (Crustacea: Anostraca) from western North America. Proceedings of the Biological Society of Washington 106:296–304.

Gibbons, J. W. 2003. Terrestrial habitat: a vital component for herpetofauna of isolated wetlands. Wetlands 23:630–635.

Gleason, H. A. and A. Cronquist. 1991. Manual of Vascular Plants of Northeastern United States and Adjacent Canada, second edition. The New York Botanical Garden, Bronx, NY, USA.

Golet, F. C., A. J. K. Calhoun, W. R. DeRagon, D. J. Lowry, and A. J. Gold. 1993. Ecology of red maple swamps in the glaciated northeast: a community profile. U.S. Department of the Interior, Fish and Wildlife Service, Washington, DC, USA. Biological Report 12.

Hanes, T. and L. Stromberg. 1998. Hydrology of vernal pools on non-volcanic soils in the Sacramento Valley. p. 38–49. *In* C. C. Witham (ed.) Vernal Pool Ecosystems. California Native Plant Society, Sacramento, CA, USA.

Hickman, J. C. (ed.). 1993. The Jepson Manual of Higher Plants of California. University of California Press, Berkeley, CA, USA.

Holland, R. F. 1998. Great Valley vernal pool distribution, Photorevised 1996. p. 71–75. *In* C. C. Witham (Ed.) *Vernal Pool Ecosystems.* California Native Plant Society, Sacramento, CA.

Holland, R. F. and S. K. Jain. 1981. Insular biogeography of vernal pools in the central valley of California. American Naturalist 117: 24–37.

Holland, R. F. and S. K. Jain. 1988. Vernal pools. p. 515–36. *In* M. G. Barbour and J. Major (eds.) Terrestrial Vegetation of California. 1988 ed. California Native Plant Society, Sacramento, CA, USA.

Jass, J. and B. Klausmeier. 2000. Atlas and Bibliography of the First State and County Records for Anostracans (Crustacea: Branchiopoda) of the Contiguous United States. Contributions In Biology and Geology No. 94. Milwaukee County Museum, Milwaukee, WI, USA.

Keeler-Wolf, T., D. R. Elam, K. Lewis, and S. A. Flint. 1998. California vernal pool assessment: preliminary report. The Resources Agency, Department of Fish and Game, Sacramento, CA, USA.

Keeley, J. E. 1996. Aquatic CAM photosynthesis. Ecological Studies 114:281–95.

Keeley, J. E., and P. H. Zedler. 1998. Characterization and global distribution of vernal pools. p. 1–14. *In* Carol C. Witham (ed.) Vernal Pool Ecosystems. California Native Plant Society, Sacramento, CA, USA.

Kenney, L. P., and M. R. Burne. 2001. A Field Guide to the Animals of the Vernal Pools. Massachusetts Division of Fisheries and Wildlife and the Vernal Pool Association, Westborough, MA.

King, J. L., M. A. Simovich. and R. C. Brusca. 1996. Species richness, endemism, and ecology of crustacean assemblages in northern California vernal pools. Hydrobiologia 328:85–116.

Kusler, J. 2003. The SWANCC decision and the state regulation of wetlands. Web page, [accessed 9 June 03]. Association of State Wetland Managers, Inc. Available at http://www.aswm.org/fwp/swancc/.

Lamb, C. 2002. Supreme Court affirms fine against Tsakopoulos. Sacramento Business Journal. December 16, 2002.

Lesica, P. 1992. Autecology of the endangered plant *Howellia aquatilis*; implications for management and reserve design. Ecological Applications 2:411–21.

McDonald, J. 2002. No charges in bulldozed-habitats case. The San Diego Union-Tribune. November 30, 2002.

Nikiforoff, C. C. 1941. Hardpan and microrelief in certain soil complexes of California. Technical Bulletin No. 745. U.S. Department of Agriculture, Washington, D.C., USA.

Novitzki, R. P. 1982. Hydrology of Wisconsin wetlands. U. S. Department of the Interior, Geological Survey and University of Wisconsin-Extension, Geological and Natural History Survey. Madison, WI, USA. Information Circular 40.

Paton, P. W. C. and W. B. Crouch. III. 2002. Using the phenology of pond-breeding amphibians to develop conservation strategies. Conservation Biology 16:194–204.

Pigg, K. B. 1992. Evolution of Isoetalian lycopsids. Annals of the Missouri Botanical Garden. 79:789–612.

Preisser, E. L., J. Y. Kefer, J. D. Lawrence, and Tim W. Clark. 2000. Vernal pool conservation in Connecticut: An assessment and recommendations. Environmental Management 26:503–13.

Preston, W. L. 1981. Vanishing Landscapes. Land and Life in the Tulare Lake Basin. University of California Press, Berkeley, CA, USA.

Proctor, V. W. and C. R. Malone. 1965. Further evidence of the passive dispersal of small aquatic organisms via the intestinal tract of birds. Ecology 46:728–29.

Purer, E. A. 1939. Ecological study of vernal pools, San Diego County, California. Ecology 20:217–29.

Raven, P. H. 1963. Amphitropical relationships in the floras of North and South America. Quarterly Review of Biology 38:151–77.

Raven, P. H. and D. I. Axelrod. 1978. Origin and relationships of the California flora. University of California Publications in Botany Vol. 72. University of California Press, Berkely, CA.

Roth, A. H. and J. A. Jackson. 1987. The effect of pool size on recruitment of predatory insects and mortality in a larval anuran. Herpetologica 43:224–32.

Ruffolo, J. 2002. The U.S. Supreme Court limits Federal regulation of wetlands: implications of the SWANCC decision. CRB 02–003. California Research Bureau, Sacramento, CA, USA.

Salve, R. and T. K. Tokunaga. 2002. Seepage response along an alluvial valley in a semi-arid catchment in north-central California. Hydrological Processes 16:65–86.

Schneider, D. W. and T. M. Frost. 1996. Habitat duration and community structure in temporary ponds. Journal of the North American Benthogical Society 15:64–86.

Schultheis, L. M. 2001. Systematics of *Downingia* (Campanulaceae) based on molecular sequence data: Implications for floral and chromosome evolution. Systematic Botany 26:603–21.

Semlitsch, R. D., and J. R. Bodie. 1998. Are small, isolated wetlands expendable? Conservation Biology 12:1129–33.

Silveira, J. G. 1998. Avian uses of vernal pools and implications for conservation practice. p. 92–106. *In* Carol C. Witham (ed.) Vernal Pool Ecosystems. California Native Plant Society, Sacramento, CA, USA.

Skelly, D. K. 1996. Pond drying, predators, and the distribution of *Pseudacris* tadpoles. Copeia: 599–605.

Skelly, D. K. 1997. Tadpole communities. American Scientist 85: 36–45.

Spencer, S. C. and J. M. Porter. 1997. Evolutionary diversification and adaptation to novel environments in Navarretia (Polemoniaceae). Systematic Botany 22:649–68.

Tasch, P. 1987. Fossil Conchostraca of the Southern Hemisphere and Continental Drift. The Geological Society of America, Boulder, CO, USA.

Taylor, W. C. and R. J. Hickey. 1992. Habitat, evolution, and speciation in *Isoetes*. Annals of the Missouri Botanical Garden 79: 613–622.

Thorp, R. W. and J. M. Leong. 1998. Specialist bee pollinators of showy vernal pool plants. p. 169–79. *In* Carol C. Witham (ed.) Vernal Pool Ecosystems. California Native Plant Society, Sacramento, CA, USA.

Tiner, R. W., H. C. Bergquist, G. P. DeAlessio, and M. J. Starr. 2002. Geographically isolated wetlands: A preliminary assessment of their characteristics and status in selected areas of the United States. U. S. Department of the Interior Fish and Wildlife Service, Northeast Region. Hadley, MA, USA. [http://www.nwi.fws.gov/Pubs_Reports/isolated/report.htm]

Wellborn, G. A., D. K. Skelly, and E. E. Werner. 1996. Mechanisms creating community structure across a freshwater gradient. Annual Review of Ecology and Systematics 27:337–63.

Williams, D. D. 1987. The Ecology of Temporary Waters. Croom Helm and Timber Press, London, U. K., Sydney, AU, and Portland, OR, USA.

Zedler, P. H. 1987. The ecology of southern California vernal pools: a community profile, U.S. Fish and Wildlife Service, Washington, DC, USA. Biological Report 85(7.11).

Zedler, P. H. 1990. Life histories of vernal pool vascular plants. p. 123–146. *In* D. Ikeda and R. Schlising (eds.) Vernal Pool Plants–Their Habitat and Biology. Studies from the Herbarium Number 8. California State University-Chico, Chico, CA, USA.

Manuscript received 23 August 2002; revisions received 17 February 2003; accepted 28 May, 2003.