Ecology, Conservation, and Management of

Vernal Pool Ecosystems

— Proceedings from a 1996 Conference —

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Based on a conference held at the Hilton Hotel, Sacramento, California

19-21 June 1996

A publication of the California Native Plant Society

Biogeography of Eight Large Branchiopods Endemic to California

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Abstract. Northern California supports eight endemic species of large branchiopods (Crustacea: Anostraca, Notostraca, and Conchostraca), three of which are listed as endangered and one as threatened under the federal Endangered Species Act. Published information on the geographic distribution of these endemics from a biological perspective is scant. This study was initiated to gain a better understanding of the biogeographic distribution and abundance of endemic large branchiopods in California. The primary objective was to investigate several physical features of wetlands that change little over time (e.g., habitat type, potential maximum and average ponding depth, potential maximum ponding surface area and water volume, soil type, and landform) for correlations to species' presence or absence. The secondary objective was to analyze selected life cycle dynamics (i.e., maximum population longevity, and minimum, mean, and maximum age to maturation and reproduction) for correlations to habitat characteristics. These objectives were accomplished by gathering and analyzing quantitative data on 5,565 wetlands studied in California between 1989 and 1996, and on endemic large branchiopods raised in mesocosms (plastic wading pools) between 1990 and 1996.

Large branchiopods were found in slightly less than half the seasonal wetlands sampled during field surveys. Anostracans comprised the majority of these. The three most common large branchiopod species were *Lepidurus packardi*, *Linderiella occidentalis*, and *Branchinecta lynchi*. Endemic species occurred in half the 50-wetland types and on most landforms sampled. Approximately two-thirds of the wetlands sampled were vernal pools. Vernal pools supported a higher percentage of large branchiopod occurrences, and species richness, than any other wetland type. The majority of occurrences of *B. lynchi* and *L. occidentalis* are located on High Terrace landforms with Redding, Corning, or Red Bluff soils; these landforms also supported slightly more than half the occurrences of *L. packardi*.

Life cycle analyses of cultured populations revealed that the Midvalley Fairy Shrimp (*Branchinecta* sp. – not described or named) has the fastest maturation period, followed by *B. lynchi*, *B. conservatio*, *B. longiantenna*, *Linderiella occidentalis*, *Lepidurus packardi*, and *Cyzicus californicus*. Overall, the seven species differed significantly in age of first reproduction (ANOVA:$F_{6,89} = 6.75$, $P < 0.0001$), and maximum population longevity (ANOVA:$F_{6,89} = 15.50$, $P < 0.0001$). However, a multiple range test revealed the anostracans did not differ significantly among each other in age at first reproduction and that *Lepidurus packardi* did not differ significantly from *C. californicus* and the four anostracan species: Midvalley Fairy Shrimp, *L. occidentalis*, *B. longiantenna*, and *B. conservatio*. Nonetheless, the age at first reproduction for *C. californicus* was significantly later than that of anostracan species. Physical wetland parameters (i.e., mean average ponding depth, mean maximum ponding depth, mean maximum ponding surface area, and mean maximum ponding volume) were utilized as predictors to assess the responses of life cycle data (i.e., mean maturation period, mean reproduction period, and mean population longevity period) using linear regression best subsets. Significant linear correlations were obtained when: mean maximum ponding surface area and mean maximum ponding volume were used to predict the response of mean maturation period ($F_{2,4} = 18.71$, $P < 0.009$); mean average ponding depth, mean maximum ponding depth, mean maximum ponding surface area ,and mean maximum ponding volume were used to predict the response of mean reproduction period ($F_{4,2} = 102.24$, $P < 0.010$); and mean maximum ponding surface area and mean maximum volume were used to predict the response of mean population longevity period ($F_{2,4} = 7.39$, $P < 0.045$).

Citation. Pages 124-139 *in:* C.W. Witham, E.T. Bauder, D. Belk, W.R. Ferren Jr., and R. Ornduff (Editors). Ecology, Conservation, and Management of Vernal Pool Ecosystems – Proceedings from a 1996 Conference. California Native Plant Society, Sacramento, CA. 1998.

INTRODUCTION

Excluding the two brine shrimp species (*Artemia monica* Verrill and *A. franciscana* Kellogg), Northern California (i.e., north of 37° latitude) supports 21 species of large branchiopods, eight being endemic to the state (Longhurst, 1955; Martin and Belk, 1988; Eng et al., 1990; Rogers, 1996) (Table 1). These endemic species include five Anostraca (fairy shrimp): *Linderiella occidentalis* (Dodds), *Branchinecta conservatio* Eng, Belk and Eriksen, *B. longiantenna* Eng, Belk and Eriksen, *B. lynchi* Eng, Belk and Eriksen, and Midvalley Fairy Shrimp (*Branchinecta* sp. - not described or named). Two are Notostraca (tadpole shrimp), *Lepidurus packardi* Simon and *Lepidurus* sp., a potential new species (J. King, pers. comm.) referred to as the Modoc Plateau Tadpole Shrimp; and one is a Conchostraca (clam shrimp), *Cyzicus californicus* Packard. Dr. Clay Sassaman (pers. comm.) is currently working on the genetics of *Cyzicus* and has suggested that *C. californicus* and *C. elongatus* may be the same animal. Therefore, *Cyzicus* species occurring in the Coast Range (*C. californicus*) and Central Valley (*C. elongatus*) were considered to be *C. californicus* for purposes of this paper. *Lepidurus packardi*, *Branchinecta conservatio*, and *B. longiantenna* have been listed as endangered and *B. lynchi* as threatened under the federal Endangered Species Act (ESA) by the U.S. Fish and Wildlife Service (USFWS) (59 Federal Register 48136) (Table 1).

In 1989, before Eng et al. (1990) had described the three federally listed endemic anostracans as species; little information was available about their biology and distribution. For this reason, Jones & Stokes Associates biologists initiated standardized data collection techniques to acquire information about potential and occupied large branchiopod habitats regarding water chemistry, plant species composition and abundance, wetland type, potential maximum and average ponding depth, potential maximum ponding surface area, soil type, and landform. It became apparent early in the investigation that water chemistry parameters were not strong indicators of the potential presence or absence of large branchiopod species because wetland water chemistry fluctuates widely, both daily and seasonally, and largely reflects local surface weather conditions (e.g., air temperature, rainfall, and wind speed and direction), photosynthesis, and soil properties. In addition, analysis of vernal pool vegetation composition as a predictor of presence (or presumed absence) of large branchiopods yielded little correlation. Therefore, we focused on physical features of the seasonal wetland, that change little if any with time, to assess species presence. Features chosen were habitat type, potential maximum and average ponding depth, potential maximum ponding surface area and water volume, soil type, and landform. This allowed comparison between wetlands without requiring temporal qualifiers.

TABLE 1. Large branchiopods (*Crustacea: Branchiopoda*) occurring in northern California.

Anostraca (Fairy Shrimp)
Branchinecta dissimilis (Dissimilar Fairy Shrimp)
Branchinecta coloradensis (Colorado Fairy Shrimp)
Branchinecta conservatio (Conservancy Fairy Shrimp)* E
Branchinecta gigas (Giant Fairy Shrimp)
Branchinecta lindahli (Versatile Fairy Shrimp)
Branchinecta longiantenna (Longhorn Fairy Shrimp)* E
Branchinecta lynchi (Vernal Pool Fairy Shrimp)* T
Branchinecta mackini (Alkali Fairy Shrimp)
Branchinecta sp. (Midvalley Fairy Shrimp)*
Eubranchipus bundyi (Knobbedlip Fairy Shrimp)
Eubranchipus oregonus (Oregon Fairy Shrimp)
Eubranchipus serratus (Ethologist Fairy Shrimp)
Linderiella occidentalis (California Fairy Shrimp)*
Streptocephalus sealii (Spiney tail Fairy Shrimp)
Conchostraca (Clam Shrimp)
Cyzicus californicus (California Clam Shrimp)*
Lynceus branchiurus (Lentil Clam Shrimp)
Notostraca (Tadpole Shrimp)
Lepidurus cousei (Intermountain Tadpole Shrimp)
Lepidurus lemmoni (Alkali Tadpole Shrimp)
Lepidurus packardi (Vernal Pool Tadpole Shrimp)* E
Lepidurus sp. (Modoc Plateau Tadpole Shrimp)*
Triops longicaudatus (American Tadpole Shrimp)

* = endemic, E = Endangered, T = Threatened

Vernal pool habitat was simulated in mesocosms (plastic wading pools) maintained out-of-doors in Sacramento, Sacramento County, California from 1990 to 1996. Large branchiopod population samples from various sites throughout California were transplanted to these pools and life-history data, including age at first maturation and reproduction, and maximum population longevity were collected for each species. Life cycle data on seven endemic large branchiopod species were analyzed to determine whether species differ in age at first maturation and reproduction, and maximum population longevity. Differences in age at first maturation and reproduction, and maximum longevity may determine differences in large branchiopod species distributions among wetlands with different ponding durations. Analysis of data collected by Jones & Stokes Associates (1996) on depth, size, volume, and duration of ponding of created and natural vernal pools indicate a very strong correlation of ponding duration to wetland depth, size, and volume. When wetland ponding depth, maximum ponding surface area, and maximum ponding volume was used as an indicator of ponding duration, I conclude that age at first reproduction and maturation, and

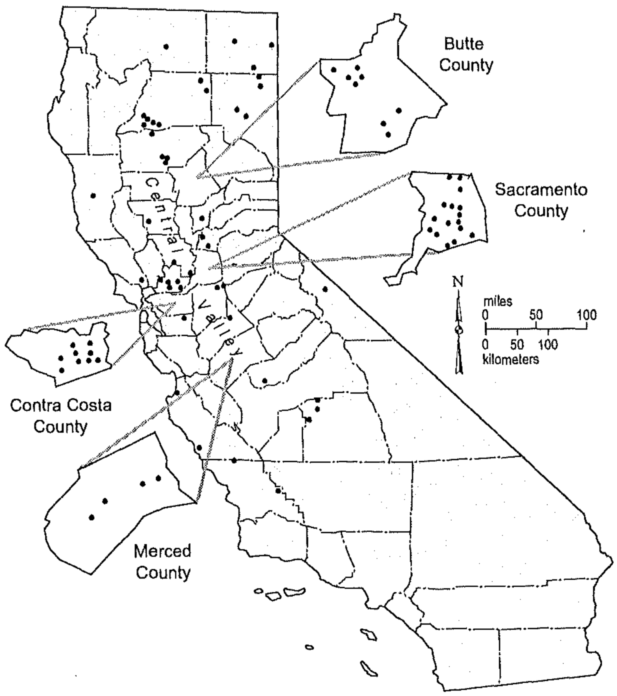

FIGURE 1. Locations of the 1996 study areas.

population longevity of the endemics may in part help explain their presence in some wetlands and absence from others.

MATERIALS AND METHODS

Field Studies

Surveys were conducted at 95 areas in 27 Counties in California (Figure 1) . Prior to September 1994, surveys for the presence of large branchiopods followed guidelines specified by Helm (1990). However, subsequent to September 1994, USFWS's listing of *Branchinecta lynchi* as threatened and *B. conservatio*, *B. longiantenna*, and *Lepidurus packardi* as endangered under the federal ESA; our work followed USFWS (1994; 1995) survey guidelines under permit number PRT-795934 of Section 10(a)(1)(A) of the federal ESA.

Two types of surveys for large branchiopods were conducted: wet-season and dry-season sampling. Wet-season sampling entailed dipnetting ponded wetlands for mature large branchiopods. All wetlands sampled during the wet season were quietly approached and visually searched for large branchiopods. Visible species were immediately captured with a D- or V-shaped dipnet (1,000 micrometer [µm] mesh pore size and 0.046 m^2 aperture size), an aquarium net (500 µm mesh pore size and 0.0452 m^2 aperture size), or a plankton net (80 µm mesh pore size and 0.01 m^2 aperture size) according to need. If large branchiopods were not observed, the wetland was sampled by systematically sweeping the net from shore to shore in a zigzag fashion across the entire length of the wetland.

The contents of each netted sample were observed for large branchiopods. Specimens were tentatively identified to species in the field with the aid of an 18x-hand lens. A representative sample was placed in a container filled with 95% ethanol, which was marked with the tentative species identification, the sample site number, and the date. Field identifications were verified in the laboratory at Jones & Stokes Associates with an Olympus SZ40 10 to 160-power zoom stereoscope, taxonomic keys (Belk, 1975; Pennak, 1978), original descriptions (Eng et al., 1990), and comparison with voucher specimens. Specimens were permanently stored in containers labeled with the collection date, location, sample number, species, and the name of the person(s) who collected and identified the specimen.

Dry-season sampling entailed collecting surface soil from the bottoms of dried wetlands and processing the soil for large branchiopod cysts (embryonic eggs) for subsequent identification. Soil samples were taken from the lowest topographic area within each wetland using a hand trowel. Depending on pool size, between 10 and 100 soil samples were taken and placed in 1-liter freezer bags for temporary storage. Laboratory analysis involved placing a single sample in a 20-cm diameter brass sieve with a 500-µm-pore-size, that was stacked on top of two other sieves (300- and 150-µm pores). The soil was loosened with lukewarm water and gently rubbed with a camelhair brush. Soil retained in the 300- and 150-µm-pore size sieves was then placed into petri dishes and examined for cysts under a 10 to 160-power zoom stereoscope or Zeiss 400-power compound microscope. Alternately, samples were placed in a brine solution: floating organic material was transferred to petri dishes and examined for cysts. Scanning electron micrographs (Mura, 1991; Gilchrist, 1978) and Jones & Stokes Associates' reference collection were used to identify the cysts to genus or species.

In the field, the following data were recorded for each wetland sampled: wetland type (e.g., vernal pool, vernal swale, stock pond, roadside ditch), potential maximum ponding surface area (m^2), potential maximum ponding depth (cm), potential aver-

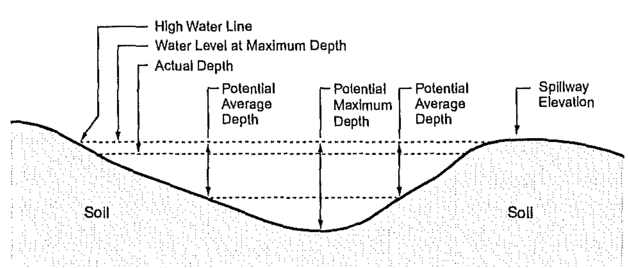

FIGURE 2. Cross section of a typical wetland.

age ponding depth (cm), soil type, and landform. Potential maximum ponding depth is the maximum depth that wetlands can potentially pond water. It is measured by the vertical distance from the ordinary high water mark or outlet elevation to the deepest point in a wetland (Figure 2). Potential average ponding depth is the average depth that wetlands can potentially pond water. It is calculated by taking several depth measurements (i.e., vertical distance from the pools' ordinary high water mark or outlet elevation to its substrate) across the wetland and dividing their sums by the number of sample measurements. Potential maximum ponding surface area was determined by measuring maximum length and width as follows: maximum ponding surface area = length × 1/n (width 1 + width 2 + width 3, etc.); n = number of width measurements. Estimates of potential maximum and average ponding depths and of potential maximum ponding surface area were measured when the wetlands were at their highest levels but not overflowing. Potential maximum ponding surface area and depth, and potential average ponding depth are approximate measurements seeking to take into account micro topographic depressions and the irregular shape of the wetlands. In addition to depth and surface area estimates, potential maximum ponding volume was calculated as follows: Potential maximum ponding volume = potential average ponding depth × potential maximum ponding surface area. Hereafter ponding depth, area, and volume referred in this paper are "potential" parameters.

Some of the wetlands were only sampled during the dry season or during periods when maximum ponding elevations did not occur. In these instances, maximum and average ponding depth and maximum ponded surface area were determined with the calculations above, using the following hydrologic indicators as reference points: the presence of high-water lines (i.e., scour marks, vegetation drift lines, distinct lines on rocks caused by water stains–mosses below the high-water line and lichens above the high-water line); the presence of vegetative cover lower than that of adjacent uplands (seasonal wetlands are typically sparsely vegetated whereas uplands have dense, grassy vegetation); and the presence of hydrophytes ("water-loving" plants) according to Reed (1988) as dominants.

Wetland names were chosen to be as descriptive as possible. According to Thorne (1984) vernal pools of California are best defined by their flora that consists for the most part of annuals. Therefore, the term "vernal" was used to indicate the abundant endemic floristic composition of the wetland that included, but was not limited to, species in the following genera: *Blennosperma*, *Lasthenia*, *Psilocarpus*, *Downingia*, and *Callitriche*. However, vernal pools were further divided into types depending upon if they were artificially constructed (e.g., artificial vernal pool) or physically disturbed or altered (e.g., plowed vernal pool, roadside vernal pool). The term "artificial" was used to indicate that the wetland was unintentionally human-made and that the construction method is unknown. Nevertheless, when the construction method was known for those wetlands that were unintentionally human-made, it was incorporated into the wetland type name (e.g., dozer scrape vernal pool). The term "created" was used to indicate the wetland was constructed for mitigation purposes (e.g., created vernal pool in ephemeral drainage, created vernal pool).

Soil information was derived from various sources, including Lambert and Southard (1992), Cosby et al. (1933), Carpenter et al. (1926), Watson et al. (1929), U.S. Natural Resources Conservation Service (NRCS) (formerly the Soil Conservation Service) soil surveys, conversations with knowledgeable NRCS staff, and, in many cases, observations made in the field while conducting concurrent wetland delineation studies for the purpose of obtaining Section 404 of the Clean Water Act permits. When NRCS mapping units and field analysis of soils disagreed with each other, field analysis was relied on due its finer resolution. Geologic formation names were based on Helley and Harwood (1985) and California Division of Mines and Geology (1965). Landform designations were derived from modern NRCS soil surveys, Peterson (1981), Hawley and Parsons (1984) and personal communications with knowledgeable individuals (T. Cook; W. Verrill).

Culture Studies

In order to gain life history data on these endemics, I collected soil samples that contained cysts and live specimens from various sites throughout California. Species populations were reared in mesocosms (plastic wading pools with a 140-cm diameter and 30 cm depth), placed on a concrete slab so as to allow full sunlight and direct fill from rainfall. The large branchiopods were allowed to hatch, grow, reproduce, and died with out any human interference, such as feeding. My observations began within 24 to 48 hours after the pools first ponded water, continued daily until the first signs of reproduction (i.e., shelled cysts in the ovisac), and then were conducted at least biweekly until the pools dried. I collected representative specimens and examined them for instar stage, sex, and presence of ova in the oviducts (i.e., first signs of maturation) and shelled cysts in the ovisac (i.e., first signs of reproduction). I gathered data including minimum number of days to reach maturity and reproduce, and maximum population longevity from 1990 to 1996. I also collected pool water quality data including temperature and pH. In addition, I obtained surface weather data recorded daily from Sacramento Executive Airport, Sacramento County (approximately 3 km northeast of the culture site) including: maximum, minimum, and mean air temperature, mean dew point, precipitation, and mean barometric pressure.

Data Analysis

Field data were originally entered into a Lotus 1-2-3 spreadsheet, then imported into Microsoft Access. A variety of selection and cross-tabulation queries were performed to determine the distribution of the species by sampling guidelines and methods, landform, soil type, wetland type, size, depth and other criteria.

Culture data were originally entered into a Lotus 1-2-3 spreadsheet, then imported to SAS or Minitab statistical programs. Analysis of variance (ANOVA) was used to compare number of days to first reproduction and maximum longevity among the endemic species, excluding Modoc Plateau Tadpole Shrimp. Life cycle data (i.e., mean number of days to first maturation [mean maturation period] and reproduction [mean reproduction period] and mean population longevity [in days]) were correlated with physical wetland features (i.e., mean average [cm] and maximum ponding depth [cm], mean maximum ponding area [m^2], and mean maximum ponding volume [m^3]) in which each of the seven species (*Linderiella occidentalis*, *Branchinecta conservatio*, *B. longiantenna*, *B. lynchi*, Midvalley Fairy Shrimp, *Lepidurus packardi*, and *Cyzicus californicus*) occurred. Linear regression best subsets was used to determine the best physical wetland variable (i.e., average ponding depth, maximum ponding depth, maximum ponding area, maximum ponding volume) to be used to predict the response of maturation, reproduction, and longevity periods. Linear regressions and fitted line plots were generated for the best subsets for each response to test if wetland depths, size, or volume could help predict endemic large branchiopod occurrences.

Results

The following presents the results of data analysis for: several physical features of wetlands supporting large branchiopods collected from field studies; life cycle dynamics of endemic large branchiopods collected from culture studies; and, correlations of habitat suitability to life cycle dynamics.

Field Studies

A total of 5,565 seasonal wetlands were sampled between 1989 and 1996. Approximately 84% (4,659) of these wetlands were sampled according to USFWS (1994; 1995) guidelines. Approximately 50% of the wetlands sampled according to USFWS guidelines revealed the presence of large branchiopods in comparison to 68.2% of the 906 wetlands sampled according to guidelines specified by Helm (1990).

Regarding the comparison of wet-and dry-season sampling: Large branchiopods were detected in 1,807 of the 4,008 (45.8%) wetlands sampled using wet-season method; 270 of the 400 (67.5%) wetlands sampled using the dry-season method; and 538 of the 1,157 (46.5%) wetlands sampled using both wet and dry-season methods. Dry-season sampling revealed a higher detection rate of large branchiopods (28.3%) in comparison to wet-season sampling (18.2%), in those wetlands in which both sampling methods were used.

The type, number, and percent of wetlands sampled are summarized in Figure 3; approximately two-thirds of these were vernal pools. Large branchiopods occurred in slightly less than half (47.5%) of the wetlands sampled (Figure 4). Anostracans occurred in slightly less than one-third (31.7%) of the wetlands sampled, followed by notostracans at 14.0% and conchostracans at 1.8% (Figure 4). The number and percent of each species of large branchiopod found within the sampled wetlands are summarized in Figure 5; together, *L. packardi*, *L. occidentalis*, and *B. lynchi* totaled 86.7% of the large branchiopods observed.

Table 2 defines those wetland types in which endemics occurred: greater than half the 50-wetland types sampled. However, 12 of the 14 sampled landforms that supported wetlands had endemic species (Table 3). Only Tidal Flat and Bolson landforms did not support wetlands containing endemics.

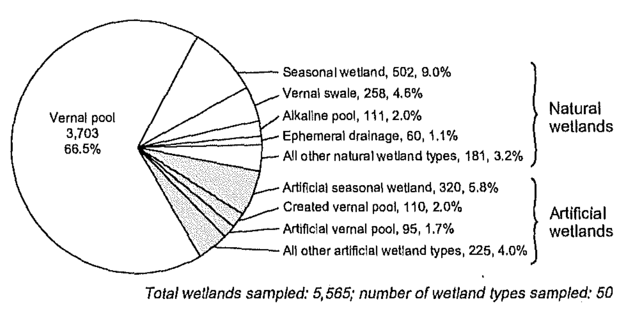

Figure 3. Type, number, and percentage of wetlands sampled.

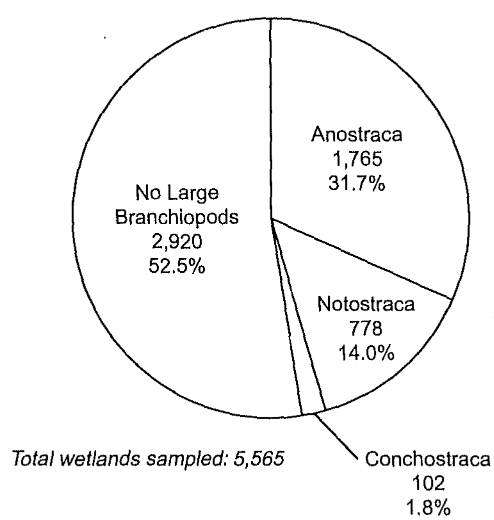

Figure 4. Number and percent of wetlands in which large Branchiopods were found.

TABLE 2. Definitions of wetland types.

Wetland Type	Definition
Alkaline pool (ALP)	Alkaline pools are scalds or nearly bare basins, sometimes salt encrusted, that are sparsely vegetated by herbaceous annual and perennial halophytic (salt-tolerant) plants, such as *Atriplex* spp., *Frankenia salina*, *Suaeda moquinii*, *Scirpus robustus*, *Distichlis spicata*, *Parapholis incurva*, *Puccinellia simplex*, and *Spergularia marina*. Pools on moderate to strongly alkaline soils are classified as alkaline pools.
Artificial seasonal wetland (ASW)	Artificial seasonal wetlands have been created inadvertently by activities such as ordnance explosions or operation of earth-moving equipment (e.g., tanks, scrapers, bulldozers, backhoes). They also may form on abandoned roads. The flora of artificial seasonal wetlands is the same as natural seasonal wetlands.
Artificial vernal pool (AVP)	Artificial vernal pools support the same flora as naturally occurring vernal pools. They have been created by similar activities as those listed above under Artificial Seasonal Wetland.
Clay flat (CF)	Clay flats are topographically distinct basins with flat, nearly level, or gently sloped surfaces occasionally dotted with soil mounds. Clay flats form in depressions where fine-grained clay accumulates through alluviation and sediment transport from adjacent higher ground and from parent-material weathering. These flats retain surface runoff from surrounding watersheds. They support vegetation distinct from that of the adjacent grasslands. The vegetation of clay flats ranges from hydrophytic to nonhydrophytic types, varying widely in relation to site topography and hydrology.
Created pool in ephemeral drainage (CPED)	Created pools in ephemeral drainages are constructed as replacements for naturally occurring pools. Shallow check dams are constructed along ephemeral drainages for mitigation purposes. Plant species supported in this habitat are similar to those of natural ephemeral drainages.
Created vernal pool (CVP)	Created vernal pools are constructed as replacements for natural vernal pools that have been lost or damaged. Shallow depressions are excavated within existing vernal pool terrain and topsoil from affected vernal pools is used as inoculum.
Ditch (D)	Ditches are constructed to drain water from surrounding uplands or wetlands. The vegetation composition of ditches varies depending on soil types, hydrology, and local climate.
Dozier scrape vernal pool (DSVP)	These vernal pools are created inadvertently from efforts to clear a fire break around existing vernal pool terrain with a bulldozer. The pools are regularly square or rectangular and support the same plant species as do existing nearby vernal pools.
Ephemeral drainage (ED)	Ephemeral drainages are small, shallow, unvegetated or sparsely vegetated watercourses with well-defined beds and banks that convey surface runoff during and shortly after rainfall. Ephemeral drainages often empty into local intermittent drainages. They support some of the same plant species associated with vernal pools and swales (e.g., *Eryngium* spp., *Eleocharis* spp.). Many have eroded to the hardpan (duripan) or claypan, leaving gravel, stones, and cobbles mixed with the remaining soil material, and thus support only sparse vegetation.
Fresh water marsh (FWM)	Freshwater marsh habitats are characterized by a dominance of herbaceous, emergent hydrophytic monocots growing in semi-permanently to permanently flooded or saturated soils. Typical plant species include *Scirpus* spp., *Typha* spp., *Sagittaria* spp., and *Carex* spp.
Percolation test pit pool (PTPP)	This habitat is created by excavating soil to create a pit for testing the water percolation capacity of the soil. These rectangular steep-sided pits are created by backhoes.
Pond (P)	Ponds are permanent to semipermanent open water bodies in natural basins with a surface area of less than 3.24 hectares and depths greater than 2 meters. Ponds support free-floating and submerged rooted, obligate aquatic plants, including *Potamogeton* spp., *Lemna* spp., and *Azolla filiculoides*.
Railroad right-of-way pool (RRRP)	Railroad right-of-way pools form in shallow depressions adjacent to railroad tracks and within the right-of-way. These habitats are usually elongated and oriented parallel to the tracks. Their depths and resulting ponding duration are occasionally increased by vehicular activity. These habitats support little if any vegetation because of their constant disturbance from herbicide spray, gravel augmentation, and vehicular activities.

TABLE 2. Definitions of wetland types (continued).

Wetland Type	Definition
Railroad right-of-way vernal pool (RRRVP)	Railroad right-of-way vernal pools are similar to railroad right-of-way pools in shape and location to railroad tracks, but they support vernal pool plant species.
Road rut pool (RRP)	This habitat is created inadvertently by vehicular activities that cause ruts in graded roads within vernal pool terrain. Road rut pools support little if any vegetation because of their constant disturbance (i.e., soil compaction and water turbidity) by vehicular activity or relatively newly created condition. When vegetation is present, it is dissimilar to vernal pool vegetation, and mainly consists of species associated with seasonal wetlands.
Road rut vernal pool (RRVP)	Road rut vernal pools are similar to road rut pools except they support vernal pool plant species.
Road side ditch (RSD)	Road side ditches are similar to ditch habitat except that they are constructed parallel to roads for drainage purposes. The vegetation composition varies depending on soils, hydrology, climate, and surrounding inoculum.
Road side vernal pool (RSVP)	This habitat is similar to vernal pool habitat except that ponding duration and vernal pool depth are increased because of downslope construction of an elevated road that acts as a berm.
Rock outcrop pool (ROP)	Rock outcrop pools form in depressions in exposed bedrock. This habitat has very thin soil (usually less than 3 centimeters deep) or lacks soils entirely, and it supports a very sparse vegetation typically found in vernal pools.
Seasonal wetland (SW)	Seasonal wetlands are shallow to deep depressions underlain by slowly permeable soils, allowing ponding or soil saturation of varying duration during wet seasons. Seasonal wetlands occur within the annual grassland matrix in swales and shallow depressions. They may also occur in isolation from other wetland habitats, within drainage systems, or adjacent to and upslope from permanent wetlands. They often fringe perennial water bodies in the zone of seasonal water level fluctuation. Similarly, seasonal wetlands can be found in swales whose outlet has been blocked. Seasonal wetlands are differentiated from vernal pools and swales by plant species composition and are dominated by exotic forbs such as *Xanthium* spp., *Lotus corniculatus*, *Rumex* spp., and *Polygonum* spp.
Stock pond (SP)	Stock ponds are semi-permanent to permanent water bodies that are constructed for watering livestock. Generally, they are made by damming ephemeral or intermittent drainages. They usually have water depths greater than 2 feet and may integrate with freshwater marsh habitat at their fringes. Vegetation composition is similar to pond habitats. Stock ponds are similar to reservoirs except they are smaller (<3.24 hectares) and shallower.
Stream oxbow (SO)	Stream oxbows form when a meandering watercourse abandons its old channel for a new one. The old channel is usually cut off from the new one by natural berms. The oxbow relies on direct precipitation, surface flow, and seasonal groundwater for hydrology. The vegetation composition varies depending on soils, hydrology, climate, and surrounding inoculum.
Vernal lake (VL)	This habitat is similar to vernal pool habitat in that it is a natural feature of the landscape and supports typical vernal pool plant species, except that the surface area of ponded water exceeds 3.24 hectares.
Vernal pool (VP)	Vernal pools are seasonally flooded landscape depressions where water ponds because of limitations to surface or subsurface drainage. Subsurface drainage is inhibited by soil layers impervious to the downward infiltration of water. Vernal pools support a distinctive vegetation adapted to periodic or continuous inundation during wet seasons and the absence of either ponded water or wet soil during dry seasons.
Vernal swale (VS)	Vernal swales are broad, shallow, seasonally wet areas that primarily convey water in somewhat defined channels rather than pool water during and after rain. Surface runoff collects in swales, wetting and saturating the soil for short periods. They often connect vernal pools, thereby filling and draining the pools. Swales often drain into ephemeral drainages. Unlike ephemeral and intermittent drainages, swales are vegetated across their bed. Poorly defined drainages meandering through gently sloped intermounds of undulating mounded topography are also vernal swales.

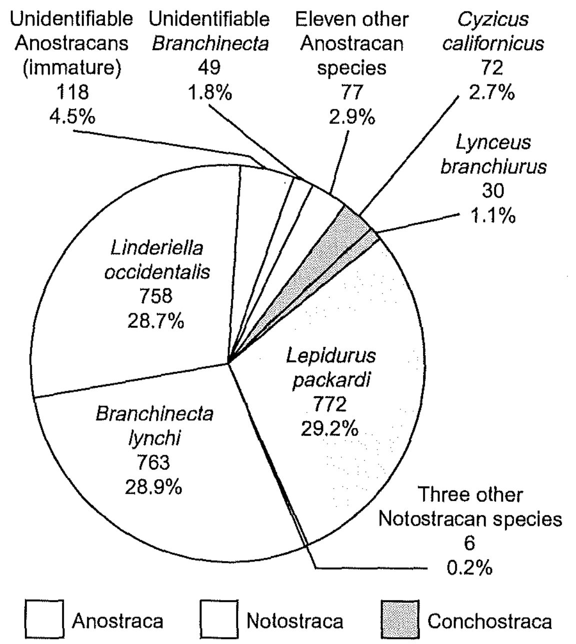

FIGURE 5. Number and percent by species of specimens from wetlands containing large branchiopods.

Lepidurus packardi occurred in 617 (16.7%) of the 3,703 vernal pools sampled, *L. occidentalis* in 617 vernal pools (16.7%), *B. lynchi* in 603 vernal pools (16.3%), *C. californicus* in 25 vernal pools (0.7%), *B. conservatio* in 13 vernal pools (0.4%), Midvalley Fairy Shrimp in 13 vernal pools (0.4%), and Modoc Plateau Tadpole Shrimp in one vernal pool (0.03%). *B. longiantenna* was not found in vernal pool habitat. Thus, greater than 15% of the California vernal pools sampled support one or more of the following species: *B. lynchi*, *L. packardi*, and *L. occidentalis*. Within the range of wetlands occupied, large branchiopods occurred most often in vernal pools: Midvalley Fairy Shrimp (92.9%), *L. occidentalis* (81.4%), *L. packardi* (79.9%), *B. lynchi* (79.0%), and *B. conservatio* (68.4%). *B. longiantenna* was found in five alkali pools and four rock outcrop pools. Of the 72 seasonal wetlands in which *C. californicus* occurred, 25 were vernal pools, 14 were created vernal pools, and 13 were alkaline pools. The Modoc Plateau Tadpole Shrimp occurred in one railroad right-of-way vernal pool and one vernal pool. Of the 14 seasonal wetlands in which Midvalley Fairy Shrimp occurred, 13 were vernal pools and one was a vernal swale. Of the 19 seasonal wetlands where *B. conservatio* were found, 13 were vernal pools, five were alkaline pools, and one was a vernal lake.

Most occurrences of *B. lynchi* (65.4%) and *L. occidentalis* (62.9%) were on High Terrace landforms with Redding, Corning, or Red Bluff soils. Greater than half the nine occurrences of *B. longiantenna* (57.1%) were in alkaline pool habitats with substratum of Angal Clay Loam on Floodplain landforms and Edminster Loam on Basin Rim landforms. The other 42.8% of the *B. longiantenna* occurred in rock outcrop pools on bedrock escarpment landforms. Most occurrences of Midvalley Fairy Shrimp (78.6%) were on San Joaquin Silt Loam on Riverbank formations within Low Terrace landforms. The other 21.4% of the Midvalley Fairy Shrimp occurrences were on Volcanic Mudflow landforms on Mehrten formations within Pentz Loams and Raynor Clay soils. Of the 63.1% of wetlands supporting *B. conservatio* where soils information was available (NRCS soil surveys are not available for all counties or for large areas within counties), 92% had substratum of Anita, Pescadero, or Peters Clay, occurring on High Terrace, Basin Rim, and Volcanic Mudflow landforms, respectively. Slightly more than half the occurrences of *L. packardi* (52%) occurred on High Terrace landforms supporting Redding and Corning soils. All Modoc Plateau Tadpole Shrimp occurrences were on Very High Terrace landforms.

Regarding pool depth, the Midvalley Fairy Shrimp typically occurs in the shallowest seasonal wetlands of all the endemics, while *C. californicus* occurs in the deepest (Tables 4a and Table 4b). On average *B. conservatio* generally occupies larger seasonal wetlands than other endemics (Table 4c and Table 4d).

Culture Studies

With regard to the life cycle characteristics of the seven endemic species (Table 5): the Midvalley Fairy Shrimp exhibits the fastest maturation period, followed by *B. lynchi*, *B. conservatio*, *B. longiantenna*, *Linderiella occidentalis*, *Lepidurus packardi*, and *C. californicus*. However, this order is slightly different when analyzing the minimum number of days required for reproduction to occur. The Midvalley Fairy Shrimp takes twice as many days to reproduce as it does to reach maturity, while *B. lynchi* takes only 1.5 as many days to reproduce as it does to reach maturity.

The observation of *B. conservatio* earliest reproduction (19 days after the pool filled with rain) occurred after a 1995 mid-April rain event in which the subsequent warm weather increased the water temperatures fairly rapidly and steady to 25° C after which all *B. conservatio* in the pool died. Its shortest longevity period of 28 days also was obtained from this same ponding event which ended 5 days after the last individual was observed alive. Another late season rain that was followed by rather warm weather occurred on April 3, 1996. During this ponding event, the shortest period to maturation (16 days) and the shortest period for population longevity (26 days) for Midvalley Fairy Shrimp was recorded. During the last few days of this ponding event, I observed live Midvalley Fairy Shrimp in approximately 32° C water.

TABLE 3. Types and numbers of wetlands and landforms in which endemic large branchiopods occurred.

Species	Wetland Type*	Wetland Number	Landforms	Landform Number
Branchinecta longiantenna	ALP, ROP	2	bedrock escarpments, basin rim, floodplain	3
Branchinecta sp.	VP, VS	2	low terrace, volcanic mud flow	2
Lepidurus sp.	RRRVP, VP	2	very high terrace	1
Branchinecta conservatio	ALP, VL, VP	3	basin rim, high terrace, volcanic mud flow	3
Cyzicus californicus	ALP, AVP, CVP, D, ED, P, PED, SP, VL, VP, VS	11	alluvial fan, bedrock, basin rim, floodplain, marine terrace, high terrace, stream terrace, very high terrace, volcanic mud flow, low terrace	10
Lepidurus packardi	ALP, ASW, AVP, CF, CVP, D, FWM, PTPP, RRP, RRRP, RRVP, SO, SP, SW, VL, VP, VS	17	alluvial fan, basin, basin rim, floodplain, high terrace, volcanic mud flow, low terrace	7
Linderiella occidentalis	ALP, ASW, AVP, CPED, CVP, D, ED, FWM, PED, PTPP, RRP, RRRP, RRVP, RSD, RSVP, SO, SP, SW, VP, VS	20	alluvial fan, basin, bedrock, floodplain, high terrace, stream terrace, volcanic mud flow, low terrace	8
Branchinecta lynchi	ALP, ASW, AVP, CPED, CVP, DSVP, DVP, ED, PED, PTPP, ROP, RRP, RRRP, RRRVP, RSD, RSVP, SO, SP, SW, VP, VS	21	alluvial fan, bedrock, bedrock escarpments, basin rim, floodplain, high terrace, stream terrace, volcanic mud flow, low terrace	9

* Wetland Types:

		ED	ephemeral drainage	RRRVP	railroad right-of-way vernal pool
ALP	alkaline pool	FWM	fresh water marsh	RSD	road side ditch
ASW	artificial seasonal wetland	P	pond	RSVP	road side vernal pool
AVP	artificial vernal pool	PED	pool in ephemeral drainage	SO	stream oxbow
CF	clay flat	PTPP	percolation test pit pool	SP	stock pond
CVP	created vernal pool	ROP	rock outcrop pool	SW	seasonal wetland
CPED	created pool in ephemeral drainage	RRP	road rut pool	VL	vernal lake
D	ditch	RRVP	road rut vernal pool	VP	vernal pool
DSVP	Dozer scrape vernal pool	RRRP	railroad right-of-way pool	VS	vernal swale

The observation of *B. lynchi*'s earliest reproduction, 23 days, occurred after a 1992 late October cool (approximately 10° C) rain event, however, the weather conditions afterwards were fairly cool allowing the longest longevity period (147 days) ending in late March 1993. Another early season cold rain which was followed by rather cool temperatures occurred in late October 1991, allowing for the maximum longevity period I observed for *L. packardi*, *C. californicus*, *B. conservatio*, and *L. occidentalis.* The shortest period to maturation for *B. lynchi* (18 days), *B. longiantenna* (23 days), *L. occidentalis* (31 days), and *L. packardi* (41 days), were recorded following a 1992 late-October rain event in which the subsequent weather was mild and water temperature highs were approximately 15° C. For *C. californicus,* observation of earliest reproduction of 43 days occurred after a 1995 late-December rain that was followed by relatively warm weather. This particular rain event and subsequent warm weather also resulted in the second earliest recording of maturation for *B. lynchi* (19 days).

The data on first day of maturation and reproduction, and maximum population longevity among seven of the endemic species: *Linderiella occidentalis*, *Branchinecta conservatio*, *B. longiantenna*, *B. lynchi*, Midvalley Fairy Shrimp, *Lepidurus packardi, and Cyzicus californicus*, conformed reasonably well to a normal distribution, and log-transformation did not improve normality in the few cases where the distribution deviated from normality. Overall, the seven endemic species differed significantly at age to first reproduction (ANOVA: $F_{6, 89} = 6.75$, $P < 0.0001$). Anostracan species had an earlier age at first reproduction than the notostracan, *L. packardi,* and the conchostracan, *C. californicus* had the latest age at first reproduction (Table 6). However, a multiple range test showed that

TABLE 4a. Average potential ponding depth of wetlands in which endemic shrimp occurred (in centimeters).

Species	Number of Pools	Mean	Range Min	Range Max	Standard Deviation
Branchinecta sp.	24	10.1	5	15	3.5
Lepidurus sp.	2	11.3	8	15	5.2
Branchinecta lynchi	605	15.0	2	122	9.0
Lepidurus packardi	568	15.2	2	151	10.5
Linderiella occidentalis	487	19.4	3	151	12.0
Branchinecta conservatio	19	19.7	10	27	5.3
Branchinecta longiantenna	7	23.1	10	40	10.3
Cyzicus californicus	70	25.5	5	91	20.8

TABLE 4b. Maximum potential ponding depth of wetlands in which endemic shrimp occurred (in centimeters).

Species	Number of Pools	Mean	Range Min	Range Max	Standard Deviation
Branchinecta sp.	14	13.7	8	19	3.80
Lepidurus sp.	2	20.7	20	20	0.23
Branchinecta lynchi	611	22.0	3	122	11.90
Lepidurus packardi	533	22.0	4	151	10.70
Branchinecta conservatio	14	26.3	13	47	9.75
Linderiella occidentalis	618	26.7	5	170	14.00
Branchinecta longiantenna	5	35.6	20	51	12.50
Cyzicus californicus	57	36.2	8	170	24.40

TABLE 4c. Maximum potential ponding area of wetlands in which endemic shrimp occurred (in square meters).

Species	Number of Pools	Mean	Range Min	Range Max	Standard Deviation
Lepidurus sp.	2	49	37.2	60	16.3
Branchinecta sp.	14	67	1.6	202	59.2
Branchinecta lynchi	697	527	0.6	44,534	2,645.4
Branchinecta longiantenna	6	678	4.6	2,788	1,133.6
Linderiella occidentalis	693	1,283	1.0	52,500	4,689.5
Lepidurus packardi	677	1,828	2.0	356,253	14,247.6
Cyzicus californicus	67	7,385	2.8	356,253	43,568.2
Branchinecta conservatio	19	27,865	30.0	356,253	80,673.0

TABLE 4d. Maximum potential water volume of wetlands in which endemic shrimp occurred (in cubic meters).

Species	Number of Pools	Mean	Range Min	Range Max	Standard Deviation
Lepidurus sp.	2	593	283	903	438
Branchinecta sp.	14	677	10	2,098	601
Branchinecta lynchi	551	13,771	1	1,618,800	90,091
Branchinecta longiantenna	6	21,819	118	111,524	44,513
Linderiella occidentalis	452	52,024	14	1,619,330	191,335
Lepidurus packardi	500	65,293	23	9,262,573	446,850
Cyzicus californicus	65	253,071	26	9,262,573	1,184,120
Branchinecta conservatio	19	651,781	300	9,262,573	2,095,663

TABLE 5. Life history characteristics of endemic large branchiopods obtained from plastic pool cultures between 1990-1996.

Species[1]	Sample Size[2]	Days to Mature[3] Min	Days to Mature[3] Mean	Days to Mature[3] SE[4]	Days to Reproduce[5] Min	Days to Reproduce[5] Mean	Days to Reproduce[5] SE[4]	Population Longevity[6] Max	Population Longevity[6] Mean	Population Longevity[6] SE[4]
Branchinecta lynchi	24	12	18.0	1.3	18	39.7	1.9	139	90.6	5.0
Branchinecta sp.	8	8	26.3	4.5	16	42.6	5.6	143	110.5	12.7
Linderiella occidentalis	25	16	32.9	2.4	31	42.8	1.3	168	138.7	3.2
Branchinecta conservatio	10	14	36.5	4.9	19	46.2	4.2	154	113.9	10.9
Branchinecta longiantenna	3	16	22.4	6.1	23	43.0	5.9	147	114.0	18.0
Lepidurus packardi	20	25	38.1	2.7	41	54.1	1.5	168	143.6	3.2
Cyzicus californicus	6	38	49.4	3.1	43	57.7	4.4	177	155.7	5.9

[1] No data available for Modoc Plateau Tadpole Shrimp.
[2] Number of populations (one population per pool) observed during a complete ponding event.
[3] First observation of maturity: at least one individual in the population has apparently functioning sexual organs (i.e., ova observed in oviduct).
[4] Standard Error.
[5] First observation of reproduction: at least one individual female in the population has two shelled cysts (this is the minimum number of cysts to complete the life cycle, assuming each cyst is a different sex thereby replacing its parents).
[6] The last individual in the population is dead.

TABLE 6. Means, 95% confidence intervals and results of a multiple range test (Student-Newman-Keuls) for age at first reproduction in seven species of large branchiopods.

Species	Sample Size	Age at First Reproduction (days) Mean	95% Confidence Interval	Multiple range test
Branchinecta lynchi	24	39.7	7.8	A
Branchinecta sp.	8	42.6	26.6	A B
Linderiella occidentalis	25	42.8	5.5	A B
Branchinecta longiantenna	3	43.0	59.2	A B
Branchinecta conservatio	10	46.2	18.9	A B
Lepidurus packardi	20	54.1	6.4	B C
Cyzicus californicus	6	57.7	22.7	C

Note: Means for species that share the same letter (A, B or C) in the multiple range test are not significantly different (P = 0.05).

TABLE 7. Means, 95% confidence intervals and results of a multiple range test (Student-Newman-Keuls) for maximum population longevity in seven species of large branchiopods.

Species	Sample Size	Maximum Longevity (days) Mean	95% Confidence Interval	Multiple range test
Branchinecta lynchi	24	90.6	20.5	A
Branchinecta sp.	8	110.5	59.9	A B
Branchinecta conservatio	10	113.9	49.4	A B
Branchinecta longiantenna	3	114.0	154.9	A B
Linderiella occidentalis	25	138.7	13.4	B C
Lepidurus packardi	20	143.6	13.2	C
Cyzicus californicus	6	155.7	30.6	C

Note: Means for species that share the same letter (A, B or C) in the multiple range test are not significantly different (P = 0.05).

the anostracan species did not differ significantly among each other in age at first reproduction and that *L.* did not differ significantly from *C. californicus* and four anostracan species : Midvalley Fairy Shrimp, *L. occidentalis*, *B. longiantenna*, and *B. conservatio* (Table 6). The age at first reproduction for *C. californicus* was significantly later than those of anostracan species.

Maximum population longevity means differed significantly among the seven species (ANOVA: $F_{6, 89} = 15.50$, $P < 0.0001$). Anostraca had a shorter population longevity than *L. packardi* and *C. californicus* had the longest population longevity (Table 7). However, a multiple range test showed that *B. lynchi* had a significantly shorter population longevity than *Linderiella occidentalis*, but that the population longevity among *L. occidentalis*, *Lepidurus packardi*, and *C. californicus* did not differ significantly (Table 7).

Habitat Suitability and Life Cycle Correlations

Pearson correlations of life cycle and physical wetland parameters in which the seven endemics occurred revealed significant linear relationships between: (1) mean average ponding depth and mean maximum ponding depth; (2) mean maturation period and mean reproduction period; (3) mean reproductive period and maximum population longevity; and (4) mean maximum ponding area and mean maximum ponding volume (Table 8).

Analysis of life cycle and physical wetland parameters using regression best subsets revealed: mean maximum ponding surface area and mean maximum ponding volume may be used as predictors for the mean maturation period and population longevity responses, respectively; and mean average ponding depth, mean maximum ponding depth, mean maximum ponding surface area, and mean maximum ponding volume may be used as predictors for the mean reproduction period response. Linear regressions of these responses and associated predictors revealed significant correlations (Table 9, Figures 6, 7, and 8).

DISCUSSION

Although the data obtained from cultures on the life cycle dynamics of these endemic large branchiopods are similar to the data collected in field and laboratory experiments by Ahl (1991), Lanway (1974), Patton (1984), Heath (1924), and Wolt (1972), it is quite variable (Tables 5, 6, and 7). Much of the variability in the maturation and reproduction data presented in this paper can be explained by variations in water temperatures which effect metabolism rates (Eriksen and Brown, 1980). The variability among species in population longevity can be explained in part by the individual species' tolerance of poor water conditions (e.g., warm temperatures, low dissolved oxygen, high algae densities). In contrast to the other endemic large branchiopods, *Lepidurus packardi* and *Cyzicus californicus* populations only died when their pools dried. Perhaps their tolerance of warm (32° C) water conditions (recorded in the field and during culturing prior to pool desiccation) may explain why these two species had the greatest population longevity periods (143.6 and 155.7 days, respectively) of the endemic species (Table 5). Nonetheless culture observations of *L. packardi* suggest that periods of maturation, reproduction, and longevity do not by themselves explain the extreme variability of the habitat conditions in which this species occurs. Simply put, how can *L.*

TABLE 8. Correlations of life history and physical wetland parameters means.

	Average Depth	Maximum Depth	Maturation Period	Reproduction Period	Maximum Ponding Area	Maximum Volume
Maximum Depth	0.913**					
Maturation Period	0.462	0.291				
Reproduction Period	0.415	0.394	0.902**			
Maximum Ponding Area	0.256	0.024	0.372	0.147		
Maximum Volume	0.321	0.084	0.491	0.281	0.990**	
Maximum Longevity	0.499	0.409	0.879**	0.837*	–0.034	0.091

Note: ∝ 0.01 r > 0.874, ∝ 0.05 r > 0.754, ∝ 0.10 r > 0.669
* significant relationship
** highly significant relationship

TABLE 9. Linear regression of life history and physical wetland parameter means.

Response	Predictors[1]	Regression Equation	R-Squared	F	P value
Maturation period	Max ponding surface area Max ponding volume	Maturation = 22.2 - 0.00602 area + 0.000280 volume	90.30%	18.71	0.009
Reproduction period	Average depth Max depth Max ponding surface area Max ponding volume	Reproduction = 46.7 -0.968 avg depth +0.385 max depth -0.000466 area + 0.000212 volume	99.50%	102.24	0.01
Population longevity	Max ponding surface area Max ponding volume	Longevity = 108 - 0.0139 area + 0.000605 volume	78.70%	7.39	0.045

[1] Predictors were chosen using best subsets regression evaluated by R-squared, C-P, and S.

packardi, having a long maturation, reproduction, and longevity period, inhabit small (2 m^2) shallow (3.5 cm) vernal pools that are not expected to pond long enough for reproduction to occur? Perhaps their high tolerance to drying pool conditions allows *L. packardi* to persist in adult form in relatively ephemeral habitats while awaiting the next storm event. Or, could these *L. packardi* have come into such a small pool by overland flooding, and the pool not actually support a population? Culture and field observations also suggest that *L. occidentalis* has a greater tolerance of warm water conditions and thus has a longer possible life span and period of occurrence than does the *B. lynchi*.

Branchinecta longiantenna is among the least understood of the endemic anostracans considered in this paper. I was only successful raising *B. longiantenna* from cysts collected from the rock outcrop pools in Contra Costa County to maturity in one out of 5 hatches. In contrast, *B. longiantenna* cysts collected from alkali pools in western Merced County produced successful cultures in two out of the two times tried. Clyde Eriksen (pers. comm.) also had no problem raising *B. longiantenna* collected from alkaline pools near Soda Lake, San Luis Obispo County. Perhaps the larval hatching from cysts of rock outcrop pools are more susceptible to warm water than those from the alkali pools. Suggestive evidence for this includes fields observations of the absence of *B. longiantenna* from rock outcrop pools when water temperatures in early-spring increased to approximately 25° C. In contrast, *B. longiantenna* have been observed in late-spring in alkaline pools containing warm (25° C) turbid water. Perhaps the species has adapted to the two extreme wetland types in which it occurs, forming two physiological races that differ distinctly in habitat requirements. Genetic and physiological studies would be useful to assess whether the populations at these different sites have diverged.

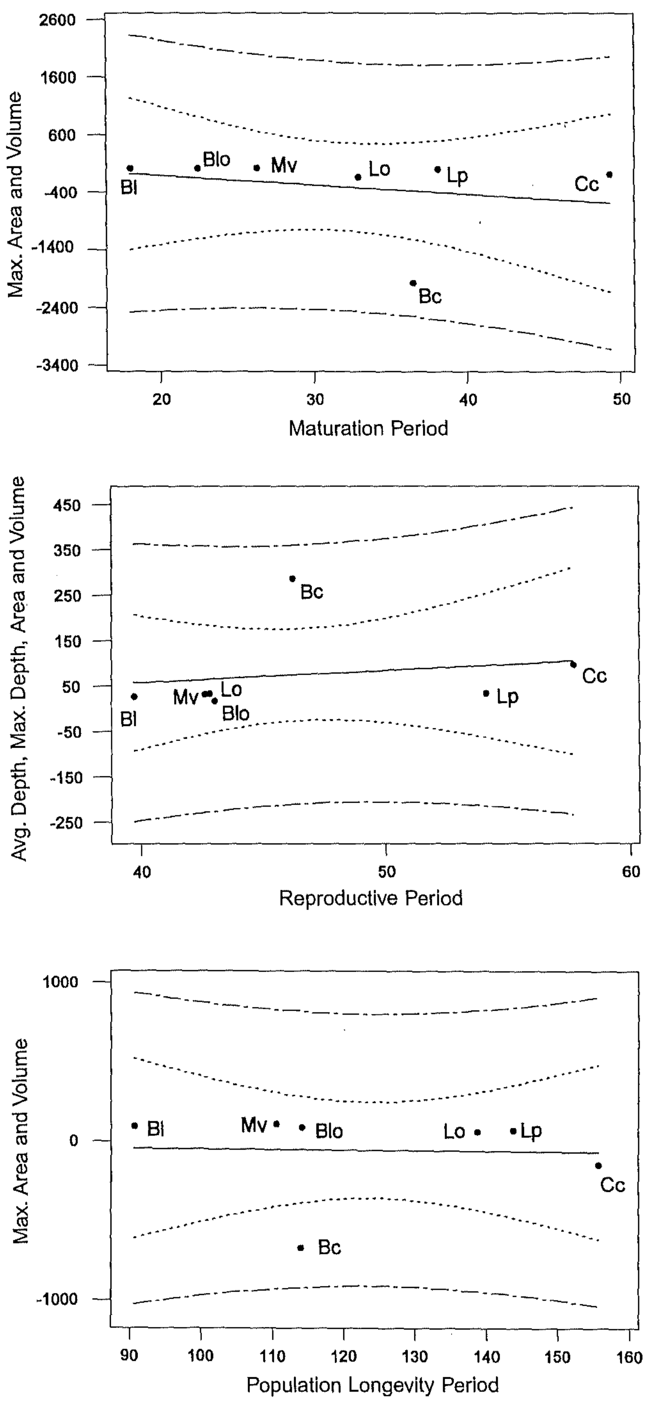

FIGURE 6. Linear regression of life history attributes and physical habitat parameters for seven endemic Branchiopods. Bc = *Branchinecta conservatio*, Bl = *B. lynchi*, Blo = *B. longiantenna*, Cc = *Cyzicus californicus*, Lo = *Linderiella occidentalis*, Lp = *Lepidurus packardii*, Mv = Midvalley Fairy Shrimp. Regression equations for each attribute are given in Table 9. Solid line shows regression while the dotted and dashed lines indicate 95% Cl and 95% Pl, respectively.

Whereas, temperature is a factor contributing to the timing of maturation, reproduction, and population longevity, other factors such as food abundance and availability, population density, and predation may also be important. Because my cultures of large branchiopods were not fed, they may have had limited nutrition thereby delaying maturation and reproduction or shortening longevity. In addition, all of the plastic pools supported very large populations (50 to 100 individuals per pool) of the locally abundant *Pseudacris regilla* (formally *Hyla*) tadpoles in the pools. These tadpoles are competitors, if not occasional predators, on anostracans. Many of the culture pools supported other predators or competitors that are common in natural vernal pools including Odonata, Dysticidae, *Culex* sp., Corixidae, Noctonectidae, and *Berosus* sp. Perhaps the protective carapace (shells) of *C. califonicus* and *L. packardi* reduce predation by insects, usually invading the pools late in the ponding season, allowing for greater population longevity.

The majority of the distribution information summarized in this paper represents data obtained from field surveys to detect the presence or presumed absence of federally listed threatened or endangered large branchiopods. However, many California Counties (or large areas within) have not been surveyed because little or no development has recently occurred or has been proposed. Therefore, additional populations and range extensions for these eight species are probable. Perhaps one reason *B. longiantenna* and *B. conservatio* have limited distributions is that the majority of wetland habitats in which they are known to occur are found on Basin and Basin Rim landforms, which are heavily impacted by agriculture and development.

In conclusion, life-history differences among large branchiopods are pronounced and are associated with differences in wetland depth, size, and volume. Wetland depth, size, and volume are consistently correlated with ponding duration (Jones and Stokes Associates 1996) and are apparently variables that can suggest large branchiopod species composition. Short-lived species that mature and reproduce at an earlier age tend to be found in smaller shallower seasonal wetlands than longer lived, later maturing and reproducing species. Variables including consistency of soil, depth of soil to impervious layer (e.g., duripan, claypan), type and thickness of the impervious layer, and local climatic factors (e.g., rainfall abundance and regularity, evaporation rates) may also effect the length of ponding. In addition, many of the endemics co-occur in wetlands, thereby suggesting a continuum of overlapping habitat requirements and distributions.

These analyses are preliminary and further study on other easily measured wetland parameters needs to be conducted to increase the precision of predicting large branchiopod species diversity in wetlands. Hopefully these and other future quantitative relationship can be used in evaluating habitat suitability for presence and absence surveys, guidance for construction or restoration of species specific habitats, and for the long-term success of management, preservation, protection and eventual recovery of these endemics. Nevertheless, because vernal pool habitats yield the highest number and species richness of endemics in comparison to other wetland types, their conservation seems mandatory for the long-term survival of these interesting creatures. Protecting a diversity of wetland types on different soil types, landforms and geologic formations will provide variations in biogeochemistry, hydrology, microclimate, soil mineralogy, soil fertility, soil formation processes, and evolutionary time scale that may be critical for dependent flora and fauna.

SUMMARY

The following summarizes what is known about the biology and geographic distribution of the eight endemic large branchiopods.

Lepidurus packardi is one of three most commonly found large branchiopods occurring in the Central Valley. The other two are *L. occidentalis* and *B. lynchi*. *Lepidurus packardi* occurs throughout the Central Valley from the Millville Plains and Stillwater Plains in Shasta County south to Merced County. It generally occurs in the same types of wetland habitat as *L. occidentalis*. Wetlands inhabited by *L. packardi* vary in size from very small (2 m^2) to very large (356,253 m^2) and exhibit extremes in depth (2-15 cm) and volume (23-9,262,573 m^3) (Tables 4a-4c).

The Modoc Plateau Tadpole Shrimp occurs in several localities on the Modoc Plateau in northeastern California. Jamie King, who is currently working on the genetics of the California *Lepidurus* species, has suggested that the Modoc Plateau Tadpole Shrimp could be a new species (J. King, pers. comm.). Morphologically it is similar to *L. packardi* and *L. cousei*. However, little is known about its biology, and our small sample size did not yield enough data to reveal significant information.

Cyzicus californicus occurs throughout the length of the Central Valley extending west into the Coast Ranges. Although *C. californicus* has not been found in as many wetland types as the three most commonly occurring species in the Central Valley: *Branchinecta lynchi*, *Linderiella occidentalis*, and *Lepidurus packardi* (Table 3); it has been found on more landforms. It also is the only endemic, considered in this paper, occurring in natural ponds. Nevertheless, because it has a relatively long maturation and reproduction period, it seems mostly restricted to habitats that are fairly deep and moderate in size thus having long ponding durations.

With the exception of *Linderiella occidentalis*, *Branchinecta lynchi* has the broadest distribution of the California endemic large branchiopods. It occurs throughout most of the length of California's Central Valley, from the Millville Plains and Stillwater Plains in Shasta County to Pixley in Tulare County. Disjunct populations occur on the Santa Rosa Plateau and near Rancho Santa California in Riverside County (Eriksen and Belk in prep). *Branchinecta lynchi* occurs mostly in vernal pools (79%), although it also inhabits a variety of natural and artificial seasonal wetland habitats, such as alkali pools, ephemeral drainages, stock ponds, roadside ditches, vernal swales, and rock outcrop pools, that occur on many soil types, geologic formations, and landforms (Table 3). Whatever the habitat, wetlands in which this species is usually found are small (<200 m^2) and shallow (mean of 5 cm). However, this species occasionally inhabits large (44,534 m^2) and very deep (122 cm) habitats as well. The short maturation period (mean of 26.3 days) of *B. lynchi* may help explain its ability to inhabit some of the most ephemeral of wetlands. Observations from field surveys and population cultures reveal young and adults dying at the onset of warm (approximately 24° C) water conditions. This may explain why the species is usually found only during cooler months.

The Midvalley Fairy Shrimp occurs in the middle portions of the Central Valley from Sacramento County south to Fresno County (Eriksen and Belk, in prep). Mike Fugate and Denton Belk (D. Belk, pers. comm.) are currently preparing a description of the species. Given the protected status history of other federally threatened and endangered large branchiopods, once its binomen becomes available, the Midvalley Fairy Shrimp's limited distribution, sparse populations, and the potential threats to its habitat make it a likely candidate for listing as threatened or endangered, under the federal Endangered Species Act. The Midvalley Fairy Shrimp may be a vernal pool/swale obligate. Approximately 93% of the wetlands in which it occurred were vernal pools; 7% were vernal swales. Similarly to *B. lynchi*, the Midvalley Fairy Shrimp inhabits the most ephemeral vernal swales and small shallow vernal pools, occurring within the intermounds of mounded micro topography, that are usually dominated by wetland grasses (e.g., *Lolium multiflorum*, *Hordeum marinum* ssp. *gussoneanum*, and *Deschampsia danthonioides*). Occupied pools are small (<202 m^2) and have average ponding depths (10.1 cm) that are less than those in which *B. lynchi* occurs (15 cm). Observations of cultured adults and young reveal both have a higher tolerance of warm water conditions than other endemic *Branchinecta* species. However, LD50 tests should be conducted to confirm. Tolerance of warm water conditions may allow the Midvalley Fairy Shrimp to take advantage of warm storm events in late spring and early summer and by maturing quickly at higher temperatures, reproduces before the aquatic habitat dries.

Linderiella occidentalis has the broadest distribution of any of the endemic large branchiopods. Except for a few disjunct populations, it mirrors that of *B. lynchi* (Eriksen & Belk in prep). Although *L. occidentalis* and *B. lynchi* often co-occur, the wetlands inhabited solely by *L. occidentalis* on average are slightly deeper (up to 20%) and larger (up to 50%) and therefore probably pond water for longer durations. This occupancy of deeper and larger habitats may be explained by the species' somewhat longer maturation and reproduction period relative to that of *B. lynchi*. With the exception of the Modoc Plateau Tadpole Shrimp, *L. occidentalis* co-occurs with all of the endemic large branchiopods considered in this paper.

Branchinecta conservatio occupies large (3,975-7,500 m^2) to very large (13,654-30,363 m^2) clay-bottomed vernal pools and vernal lakes (356, 253 m^2) on Tuscan and Merhten geologic formations and on Basin Rim landforms in Tehama, Merced, and Solano Counties, respectively. In western Merced County, it occurs in medium (1,394-3,903 m^2) to very large (52,500 m^2) alkali pools on Basin and Basin Rim landforms. Because of the large wind-exposed surface area and fine substrate within these pools, they are generally turbid. The turbidity decreases photosynthesis, thereby contributing to the pool's sparsely vegetated condition. Yet the Conservancy fairy shrimp is associated with endemic vernal pool grasses, including Colusa grass (*Neostapfia colusana*) and Orcutt grasses (genus *Orcuttia)* that are found in large deep vernal pools that pond continuously for many months, which may perhaps be explained by its relatively long period of maturity (mean of 36.5 days) and reproduction (mean of 46.2 days). However, data collected in Butte County by Carolyn Brown (pers. comm.) revealed the presence of *B. conservatio* in three small (250, 170, 30 m2) but moderately deep (10, 15, 27 cm) vernal pools. Nevertheless, *Branchinecta conservatio* usually co-occurs with one or more of the following species that also have relatively long maturation and reproductive periods: *Linderiella occidentalis*, *Lepidurus packardi*, and *Cyzicus californicus*.

With the possible exception of the Modoc Plateau Tadpole Shrimp, *Branchinecta longiantenna* has the most limited distribution of the endemic large branchiopods considered in this paper. It is known to occur in clear, moderately deep (20 - 46 cm), small (4.6 m^2 - 74.4 m^2) to medium size (2,788 m^2) pool depressions in bedrock outcrops in Contra Costa and Alameda Counties; moderately deep (15- 40 cm), medium- to-large sized (2,788 - 8,364 m^2) turbid alkali pools at the Kesterson National Wildlife Refuge in western Merced County; and similar habitats surrounding Soda Lake in San Luis Obispo County. Its occurrence in two extremely dissimilar habitats is puzzling.

ACKNOWLEDGMENTS

I thank Jim Woollett from Lawrence Livermore National Laboratory for habitat information on *Linderiella occidentalis,* Steve Leach from Woodward Clyde Consultants for habitat information on *Branchinecta lynchi*, Carolyn Brown from the California Department of Transportation for habitat information on *Branchinecta conservatio*, and Michael Peters and Dennis Woolington of the San Luis National Wildlife Refuge complex for important habitat data on *Branchinecta longiantenna* and *Branchinecta conservatio*, species for which limited information presently exists, and for the opportunity to view these two species in their natural habitats.

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