other than bovines and birds on their lands. In an aquatic survey of the Sacramento NWR **west** of the Sacramento River at the border of Glenn and Colusa counties, refuge biologist Joe Silveira turned up three species of fairy shrimps already known from the region, *Linderiella occidentalis, Branchinecta conservatio*, and *B. lindahli*. Unexpectedly, *B. coloradensis* also debuted in one of their pools, a location that is only its third known site of residency in the Central Valley. Further to the south, and west of Merced, lies the San Luis NWR Complex. Of 59 sites sampled in 1994, including both sides of the San Joaquin River, 15 pools **west** of the river yielded anostracans. Here too, most were *Branchinecta lynchi*, but the Kesterson area also produced *B. conservatio, B. longiantenna*, and *B. lindahli*. Do such collections suggest that wildlife refuges hold the remains of the aquatic resources west of the Central Valley's major rivers, or are these records, and the few we have from other surveys, "the exceptions that prove the rule" that fairy shrimps are scarce west of the major rivers in California's Central Valley? Let's ask the talk-show hosts, certainly they will have the answer!

While still peering westward, take a look again at Map 4.1 (p. 58). As you study it, you will probably be struck by the paucity of anostracans in the North and Central Coast Ranges and the near absence of our fine phyllopodous friends in all coastal counties from Santa Cruz to the border with Oregon. Why should this be? Our best guesses (yep, here we go again) are insufficient aridity and lack of pool sites, consequences of the area's generous rainfall. The sites we know about are in meadows, on a depositional flood plain, or along the San Andreas Fault, places which runoff from excessive precipitation could probably not soon erode or fill in. Pools, if present, probably don't freeze or desiccate sufficiently given the cool but not cold near-coast locations and frequent rains. As one trends southward, rainfall and its frequency lessen, and wave-cut terraces, which over geological time have been lifted above the sea, provide an increasing number of pool basins, most numerous in southern-most San Diego County.

Further evidence that fairy shrimps aren't everywhere is presented in a report by Sugnet and Associates (1993). They demonstrated that only about 27% of possible habitats in the northern two-thirds of the Central Valley contained anostracans (830 pools of 3,092 visited). Interestingly, in Sacramento County where 20-30 pools were sampled in each of several clusters of pools, about 75-85% yielded fairy shrimps. These high frequencies were clearly the exceptions for, not uncommonly, **none** were taken in areas where, for example, 95, 86, and 56 sites were visited. That these results closely portray reality is supported by the work of Brent Helm at Jones and Stokes Associates, Sacramento (in press). Brent sampled 5,565 seasonal wetlands in the same region; fairy shrimps paddled their way through only 31.7% of them.

The story is no different in southern California. Near Oceanside in San Diego County, pool basins lie scattered across the coastal plain. While many are natural, a substantial number are considerably deepened by human activity, or are man-made. Some are habitats for anostracans, others not. Truly baffling is the oft-repeated situation where one site will contain fairy shrimps while its seemingly identical neighbor a meter or so distant harbors **nothing**.

These kinds of perplexities are repeated on the grassy slopes of Cachuma Canyon in the backcountry near Santa Barbara where, for 40 years, Clyde has casually kept track of four earth-slump pools within a km of each other. To the eye, all basins are formed in the same soil type. They fill faithfully each year, yield similar water chemistries, and probably dry up at about the same time. All are frequented and dumped upon by cattle. Two pools with milky-colored water contain fairy shrimps. The clam shrimp *Cyzicus californicus* lays claim to a more turbid habitat. Several meters from the latter is a pool of clear water, somewhat smaller but just as deep, harboring no anostracans, although a few clam shrimps were seen in it once. Clyde led Don Wootton to this area in 1954. We collected two kinds of fairy shrimps. One with red eyes was then called *Pristacephalus occidentalis*; you know this little beauty today as *Linderiella occidentalis*. We had no idea what the other species was, and rightfully so, because *Branchinecta lynchi* was not formally described until 36 years later by Eng, Belk, and Eriksen (1990). At any rate, the contents of these pools, one containing both species but the other with only *B. lynchi*, have apparently not changed over the years. What's going on? Since these species not infrequently co-exist, why aren't they together in both sites in Cachuma Canyon, and why haven't they invaded the other pools? Similar questions have been expressed in the scientific literature by scientists whose intellectual curiosity has been challenged by these rain-pool critters. So far, in this regard, all of us have met our match.

Because small basins of water are largely inaccessible from view along the few roads in the Santa Barbara backcountry, and in hopes of finding more rain pools in topography similar to that in Cachuma Canyon, Clyde cajoled his psychology-professor friend and pilot, Harv Wichman, to fly him over the slopes of the San Rafael Mountains from Fillmore to Santa Maria (and ultimately over much of California south of Monterey). Ecstatically we noted a grassy hillside north of Ojai which sported about a dozen pools. They appeared to be formed as earth-slumps, just as were those in Cachuma Canyon; in fact, this hillside could have been mistaken for Cachuma Canyon! On the ground, and wondering which species would be found where, we began dip-netting the pools. After several hours of diligent work, disappointment set in because we collected nary a shrimp. Even water fleas (Cladocera), creatures "typical of almost every pool", were absent. This was a strange place! Or was it? Remember, fairy shrimps are not found everywhere, even in the heart of "fairy shrimp country". The question remains ...**why**?

Road-side ditches serve as homes for fairy shrimps; well, that is to say **some** do. **Most don't!** On one trip in the Alturas area of far northeastern California, Clyde dip-netted every ditch he saw, and not one fairy shrimp was found. By contrast, in the northern portion of the Central Valley, that is, in the heart of "fairy shrimp heaven", of 218 road-side ditches sampled, 55 (25%) had fairy shrimps, most of which were *Linderiella occidentalis*, but 11 harbored or co-harbored *Branchinecta lynchi* (Sugnet & Associates 1993). Interestingly, these data are heavily skewed by the situation in Sacramento County, where 30 of 37 ditches possessed *Linderiella*, including two which also harbored *B. lynchi*. What this means is that, elsewhere, fairy shrimps occur in only 14% of road-side ditches – hardly a preferred habitat type it seems. According to the Federal Register (1994), most, if not all, of Central Valley ditches containing anostracans are probably remnants of vernal pools. If true, then man-made road-side ditches, by themselves, seem to be lousy residences for our selective subjects.

In our experience, the general absence of anostracans in ditches is related to soil, which in turn affects water chemistry. Ditches are usually constructed by scooping away the topsoil. The leached, more acidic sub-soil seems to provide inappropriate habitat. However, we, and others we have spoken with, have noted that where the top 6-8 cm of material have been carefully returned and kept in place, or carried in by erosive waters, for example along desert roads, fairy shrimps occur more commonly, although still infrequently.

Several studies in the Midwest and one in Canada have demonstrated that an anostracan's presence or absence one year is not necessarily the situation forever (e.g., Dexter & Kuehnle 1951; Donald 1983). Remember, fairy shrimps respond to distinct, species-specific environmental clues that, when received, result in hatching of some of the cysts in the pool's sediments. If a species of fairy shrimp is not present in any one year, we cannot say with certainty that none dwell in that particular place. Perhaps rain or temperature patterns proved to be unsuitable that season. Similarly, if fairy shrimps are present one year, it is just as inappropriate to claim they will be there forever, as for example in a pool constructed for mitigation. The rationale is that species may survive for a year or so in a marginal habitat, only to be eliminated by continuing poor conditions.

Certainly some pools seem to have had fairy shrimps "forever"; for others, we do not usually understand whether their absence suggests inappropriate environmental clues, extinction due to a series of "bad years", or a just plain unsuitable habitat. Likewise, how often such "barren" pools are successfully reinvaded is another unanswered question. My gosh, if humans are so unpredictable, how can we expect fairy shrimps to be otherwise? And if there are so many unanswered questions, let us humans of all ages, abilities, and backgrounds, get on with the fascinating sleuthwork of ferreting some of them out.

How fairy shrimps got where they've got

Okay, so fairy shrimps aren't in every pothole, puddle, pool, pond, pan, or playa you can shake a stick at, but they are found in some of the most "out of the way" places! Consider the miles of water between the mainland and California's Channel Islands, where, yes, *Branchinecta lindahli* swims in rain pools (Soiseth 1994)! Then visualize the myriad of wilderness-area snowmelt-filled basins along the Sierra crest, far from road ends or trail heads, that are graced each year with fairy shrimps paddling in isolated splendor and oblivious to human wonderment about how they got where they got. Several hundred miles away in the far northwest corner of the State, the Siskiyou Mountains harbor, as far as is known, two populations of *Streptocephalus sealii*, isolated by distance, topography, climate, and who knows what else, from others of its species, and populations of other species. Contrast these wet coastal mountains with the hot, comparatively desolate, and seemingly inhospitable expanses of California's deserts, and one is amazed to find that when suitable conditions present themselves, fairy shrimps are often in residence.

How did our anostracan friends get to these places given what seem to be improbable odds, given such distances, and given such inhospitable territory and seasons in between? And when did they arrive, yesterday, or in ancient times? If it was long ago, and under conditions scripted by different land forms, were the distances as great, the territory in between as inhospitable? These are fascinating questions about which any of us can conjecture on a rainy afternoon, but, whether pool sites be near or far, remember, fairy shrimps are adapted to those which desiccate, and the mechanism anostracans use to withstand desiccation is the cyst. Being resistant and tiny (about 0.15-0.40 mm in diameter), cysts are the structures that get transported from place to place.

The major agents of dispersal are two. First, cysts are known to pass undamaged and undigested through the digestive tract of birds (Proctor *et al.* 1967). The "how-I-got-there-from-here" story begins when mature female anostracans, containing cysts in their ovisacs, are eaten by birds. When our fine feathered friends take wing and fly to other aquatic locales and there charitably void their intestinal holdings, the result might be inoculations of sites new to fairy shrimps. But then the pools must desiccate, be refilled, and finally present the appropriate mix of temperature and water chemistry to prompt hatching. Undoubtedly a number of such "inoculations" go nowhere because the suite of conditions are, and remain, unsuitable for some of the species that just happened to be deposited. Obviously some are successful, and the sprinkling of the arctic fairy shrimp, *Branchinecta paludosa*, down the Rocky Mountain chain is thought to reflect the effectiveness of dispersal by bird-discharge (Saunders *et al.* 1993)!

A second mechanism, with most of the same limitations and possibilities for success, is the transfer of cyst-containing mud on the feet or feathers of birds. Mud, particularly if attached to migrating waterfowl, offers the possibility of long-distance transport before it is washed off in some distant pool along the flyway. By contrast, cysts passing down a bird's gut will be discharged, perhaps in an aerial bombardment far from water, within about 1.5 hours after feeding, although a small number may still be in the feces for up to 24 hours (Proctor *et al.* 1967).

Although aquatic birds are the most likely agents of dispersal, large, migratory mammals are also known distributors. Many of these beasts "wallow" in dirt, using the dust as a sort of desiccant for lice and other skin-infesting creatures. Wallowing in the same place deepens the basin and maintains a dust supply by continually abrading the soil, activities which discourage growth of plants which would bind the soil if present. Known in the Midwest as "buffalo wallows", these basins had their equivalent in California until the turn of the century in the form of elk wallows. Such depressions fill with rain and often harbor fairy shrimps. Thus cysts, when present, may get caught in the fur of rolling animals and be transported to another wallow where some may be left behind. Mud embedded in an animal's hooves, possibly containing cysts, could also be carried from water hole to water hole (Thiery 1991). And, finally, hearty gulps of water, perhaps containing gravid females, could allow gut-transfer, for if cysts are passed through the digestive system of birds unaffected, undoubtedly they can make safe passage down the guts of other vertebrates. Of course, "deposits" are made whenever and wherever the urge strikes, possibly in a basin suitable for fairy shrimps, possibly in a watershed where flooding carries cysts to a suitable home.

Various other creatures in addition to birds and mammals also eat fairy shrimps, and also indiscriminately purge themselves of the indigestible remains of their meals. What about these creatures? Well, it turns out that some inquisitive souls have delved into this more private aspect of frog and salamander biology. Both a French and a Louisiana scientist fed gravid fairy shrimps to lab-bound frogs, then succeeded in hatching nauplii from cysts recovered from their excrement (Mathias 1937; Moore 1973). Out in the real world, Thiery (1991) found viable cysts in the gut contents of salamanders which he caught in Moroccan pools inhabited by fairy shrimps. We were unaware of crayfish waltzing through California vernal pools until Brent Helm told us of seeing them on several occasions in pools in Sacramento and Yuba counties, so merely as a reminder that we should not overlook any possible mechanism of movement, we inform you that a wonderful father of fairy shrimpology, Walter Moore, teamed up with a student to see if Louisiana crayfish (crawdads in their vernacular) might be distributive agents. They fed cyst-bearing female *Streptocephalus sealii* to crayfish, and, guess what, out came cysts, still viable after their seemingly inhospitable journey down a gut containing one of the more formidable grinding structures known in the animal world, the gastric mill (Moore & Faust 1972).

Other transfer agents do exist, although their occurrence must be much less common, their direction random, and their success definitely obscure. Still, here are some remote possibilities. Unusual flooding, particularly in flood plains adjacent to large rivers (e.g., in California's Central Valley à la January 1997), may overwhelm pools and sweep cysts or wriggling fairy shrimps across the landscape or down water courses. Certainly most are buried or stranded in unsuitable places, but by some remote chance, should they end up in shallow basins, a new population may develop if the suite of conditions necessary for success is ultimately and appropriately presented.

In deserts, where winds are strong and vegetation sometimes minimal, an unlikely possibility is that soil and cysts may be bounced relatively unimpeded across the desert floor to a different site. A more plausible distributive agent is the so-called "dust devil", a small cyclonic wind that is strong enough to swirl fine soil particles, debris, and undoubtedly cysts, high into the desert air and carry them erratically across the landscape. Once again, blind chance may find an ideal spot for the cysts, though more probably they will be lost in the desert's unsuitable vastness.

Under historical conditions, wind-transport of desert species was probably less likely than today. Although cysts are deposited on top of a pool's bottom, being larger and heavier than surface clays they get worked into the sediment by water movement caused by persistent winds. Therefore, when the pool dries, cysts are trapped and bound in the soil about 5 mm below its surface (Eriksen *et al.* 1988a), inaccessible to the force of the winds. However, in today's world of ORV, military, and commercial use of dry desert basins, surface sediments are constantly abraded. Such abrasion and compression not only destroy some of the buried cysts, but loosen the soil to such an extent that removal by wind is far more successful (Eriksen *et al.* 1988a).

These same vehicles, forcing their way through mud in one wet basin then heading out for more challenges at another, must also carry, and drop, cyst-containing mud along their route, possibly in another basin, certainly on the floor of the garage. And to prove that the latter is not a facetious statement, Steiert (1995) recounts the story of a woman, living on the Texas High Plains, collecting a jar full of fairy shrimps from a rain puddle in her concrete driveway.

That transfer of cysts from pool to pool or success of cysts once transported are not particularly common events (Belk & Cole 1975) is suggested by the following: Certain species are highly restricted in distribution; adjacent pools may have different or no fairy shrimps; pools observed year after year seem always to house the same species, or mix of species; and structural and genetic studies demonstrate population differences between regions (Dumont *et al.* 1991) and sites (Baskin 1994; Fugate 1992; King *et al.* 1996). The fact that fairy shrimps are not everywhere is also possible evidence for the uncommon nature of transfer.

How often species have reached a habitat, then been lost to drought, competition, or some other ecological reality, only to be reintroduced once more, is certainly grist for the inquiring mind and for research.

Categorizing California's environmental diversity: An overview

We hope we have made it clear that we know where some fairy shrimps are sometimes, and where others seem to be all of the time. In an attempt to make sense out of the differential distributions of California's anostracans, and the ecological reasons for those distributions, we have developed a classification of **pool-basins** (p. 66), and grouped our state's 23 species according to what we call **habitat categories** (Table 4.1, p. 70). These are defined by pool characteristics which add to the general ecological conditions found within the eight **geographic-vegetational regions** of California (Map 4.2, p. 68).

But first, if you are not particularly conversant with California's host of environments, it certainly behooves us to introduce you to them! Such a task is not an easy one, however. Many individuals have wrestled with a way to organize the state's incredible ecological diversity into some conceptually useful framework. For others the task seemed rather simple. As an example of the latter, if you were to ask even long-time residents about the state's climate and space, many would give you the usual PR about "endless summer", sandy beaches, the hills of San Francisco, and maybe the geological and meteorological reasons for last year's vintage of late-harvest Zinfandel in the Napa Valley. Like a couple of dots on your TV screen, these few dots on a map of the state are but a tiny part of the picture of California, meaningless as far as fairy shrimps are concerned, for none of these fine creatures dwell any longer on such prime real estate. Additionally, by themselves, these fragmentary descriptions give a distorted view of this grand state and offer no hint about the juxtaposition of different land forms, the variations in climate that these conditions help create, or the distribution of anostracan species determined to a great extent by them.

Those who do see the complexity would tell you California is an amazing piece of this planet! And it probably contains, somewhere, a microcosm of most of the geological wonders found spread over the face of earth. It is more diverse in topography, geochemistry, climate, and vegetation than any similarly-sized chunk of our globe's crust. The isolation of its many living things by ocean, elevations, and deserts has produced a rather amazing and enviable list of fascinating plants and animals, including fairy shrimps, that are found nowhere else!

Those same knowledgeable people would also add that traveling across California is like riding a giant roller coaster, no matter which route is chosen. Were you to select the central two-thirds of California to test that point, and hop aboard your car where the mighty Pacific pounds against the land, almost immediately you must traverse the Central Coast Mountains, 900-1,500 m high, to get to the enormous Great Central Valley. Once the Central Valley is crossed, 75 km wide, almost 700 km long, and most of it less than 150 m in elevation, the lofty Sierra Nevada awaits to be scaled. The "Range of Light" forms a giant backbone along a considerable length of the state. Over 600 km from end to end, and most of it 2,750-4,250 m in height, it is topped by 4,418-m Mt. Whitney. This gigantic monolith of granite rock juts skyward more than any other point of land in the lower 48 states. Amazingly, only 140 km by air to the east, near the Nevada border, our roller coaster will plummet into the lowest spot in North America, Death Valley, some 86 m below sea level! However, no simple single slide, this one. First, there is a descent of over 3,050 m in only 20 km into the deepest part of the Owens

Valley. Then it's back up again to 3,368 m and the top of Telescope Peak, crown jewel of the Panamint Range, before dropping into the finality of Badwater, Death Valley's lowest spot.

While mulling over the changes in elevation just described, try to imagine the changes in temperature, rainfall, length of seasons, or any other environmental condition that parallels such drastic differences. Then, let your mind retrace the variation in land form from the Pacific Ocean to Death Valley. Over this distance, temperatures will range from year-around mild conditions near the 1,600 km-long coast, to subfreezing winters in the Sierra Nevada, to oppressive summer heat in Death Valley. Precipitation will vary drastically, from almost rain-forest amounts near the north coast to trace amounts in Death Valley, and most of it comes from winter storms of arctic origin. Virtually none falls during summer. The low desert of southeastern California is the sole exception, with the majority of its minimal rainfall arriving with summer storms which have their origin in the Gulf of Mexico (Major 1977).

Now that your roller-coaster ride has acquainted you with some of the fantastic geographic changes that California presents, how do you organize it all in your mind? As an aid, let us note some of the attempts that others have made to consolidate the state's overwhelming geologic and biotic diversity into some conceptually useful scheme. Various researchers have divided California into "provinces" based upon differences in landform (Durrenberger 1968), in vegetation (Stebbins & Major 1965; Munz & Keck 1973; Major 1977), and in fauna (Van Dyke 1919). With regard to such classification schemes, and for the purposes of this book's topic, the known distribution of California fairy shrimps correlates best with a modification of the vegetational subdivisions utilized by Stebbins and Major (1965). Those subdivisions and their modifications were described by Eng, Belk, and Eriksen (1990), and comprise eight **geographic-vegetational regions**: North Coast Mountains, Cascade-Sierra Nevada Mountains, Great Basin Desert, Great Central Valley, Central Coast Mountains, South Coast Mountains, Mojave Desert, and Colorado Desert (elaboration beginning on p. 67; Map 4.2). These eight regions can be geographically and vegetationally defined because they are generally set apart by topographical boundaries (mountains). Our presentation of these regions is organized along the continuum from high elevations and latitudes with cold temperatures, to low elevations and latitudes presenting high temperatures.

Reasonably superimposed upon the geographic-vegetational regions are what we call **habitat categories**. These help define the pools in which fairy shrimps actually dwell by adding to the gradients of the regions' characteristics the variables of low to high dissolved salts, greater to lesser predictability of filling, and long to short duration times (Table 4.1, p. 70). We champion these habitat categories for an important reason. All too commonly, little, and often fragmentary, specific habitat information is available for many of the California species. However, one might reasonably judge at least the general suite of conditions which a species faces by knowing the properties of the particular habitat category in which it is found. Let us illustrate. Some of the California species are rare; others occupy remote areas. In both cases, little is known about physical and chemical properties of their pools, and often not even casual descriptive information is available concerning their habitats. Additionally, some fairy shrimps occupy several types of basins, but existing habitat data, including out-of-state information, may represent those types unequally thus biasing one's perception of a species. By knowing the habitat category applicable to a particular species, one can make a reasoned guess about the spectrum of environmental conditions that exist there, in spite of a lack of specific data. Additional information describing conditions in which anostracans dwell can come from knowledge of the soils or rocks underlying these **pool basins** and of the way the basins were formed.

Because the subject of our book is the **Fairy Shrimps of California's Puddles, Pools, and Playas**, it may sound as though we are adhering to a commonly accepted scheme of defining, and therefore classifying, smaller bodies of water. If so, what **are** the differences between puddles, pools, and playas, and where do ditches, stock tanks, solution pits in rocks, and gas chambers in lava flows fit into the scheme? You might feel that such a question is unimportant, for after all these words are colorful and conjure up pictures in the mind that do a good job of portraying some types of seasonal water bodies. Problem! Speak to a rancher, Fish and Game biologist, university ecologist, or even your authors, and you will undoubtedly encounter a diversity of descriptions and definitions that may not include your own. If there is not a universally accepted classification, then how can we usefully talk about which fairy shrimp species are found in what kinds of aquatic habitats? Eng, Belk, and Eriksen (1990) attempted to deal with that problem by constructing a classification of temporary waters that was suited to the ecology of anostracans. In the next section of this chapter we present that scheme.

But first, please note, we organize the types of **pool basins** and **habitat categories** as we do even though we recognize that some fairy shrimps are generalists and are not constrained by the way our tidy minds group the places in which they dwell. When we consider such a widely-distributed species, we will do so in the context of the habitat category in which it **most commonly** occurs in California, with mention of course of the range of localities and basin types in which it is known to appear. In these ways, then, we will describe in Chapter 5, **Natural history of California's species of fairy shrimps**, what we know, and what we hypothesize, about the biology and the ecological requirements of the Anostraca of California.

A classification of pool basins where fairy shrimps might dwell

Our classification scheme of possible fairy shrimp waters is not necessarily dependent upon, or restricted to, specific geographic-vegetational regions or habitat categories. This three-tiered plan allows flexibility in accommodating special characteristics of specific sites. The tiers are hydrological, formational, and locational/descriptive.

In the **hydrological** tier we recognize three types. **Seasonally astatic** pools are those that fill and redry one or more times during any year, depending on the seasonal nature of precipitation and drought. **Perennially astatic** sites fluctuate significantly in level during the year, and as a result a portion of the bed dries out, but the entire body of water does not disappear completely every year (Decksbach 1929, translated by Hartland-Rowe 1972). **Aestival** habitats are shallow and semi-permanent in the sense that they retain some water year-long, but freeze to the bottom during winter (Daborn & Clifford 1974).

Understanding the **formational** origins of pool-basins is often important to the understanding of their water chemistry and seasonal change, and perhaps ultimately to putting damaged or destroyed systems back together. Therefore, recognizing that a temporary pool is **not** just any simple dimple or subtle puddle on the face of the land that receives and holds water for a period of time is of paramount importance!

Although formational origins of pool basins are varied and complex, they are usually either a result of geological processes (**geogenic**), some of which are no longer active in California (e.g., glaciation), or of organisms "doing their thing" (**biogenic**). Categorizing pool basins under these two headings gives us a colorful list of descriptive names like: lava flow dam pools, sag ponds, cirque lakes, swale pools, animal wallows, stock ponds, borrow pits, and bomb craters. For a wonderfully readable survey, we refer you to Norwick (1991) who has described, largely from the standpoint of geological processes, how an array of pool basins came or may yet come into being in California.

The **locational/descriptive** tier within our classification allows general and inclusive comments which describe conditions at a particular site (e.g., desert, grassland, coniferous forest, alpine, snow-melt, or rain-pool). However, they may also refer to unique regional pool-types like the famous **California Vernal Pools**, identified by their largely endemic annual plants (Thorne 1984). We ask you to take note of this distinction, for many of California's temporary bodies of water, though referred to casually and incorrectly as vernal pools, are **not** because they form at times other than spring, or have no resident endemic plant species.

Although this scheme offers a way to classify the types of basins in which pools form, and knowing the origin of a basin and its soils is an ultimate goal, we do not want to leave the impression that every, or even any, collector of fairy shrimps will be able to decipher all the various clues that place each pool into each hierarchical category. As is usual in environmental matters, some things are known, others are reasonably guessed at by those with appropriate expertise, and much lies in the realm of the unknown. Still, we offer this classification for your consideration in an attempt to be inclusive, understanding that California fairy shrimps may not yet have been found in all possible types of basins.

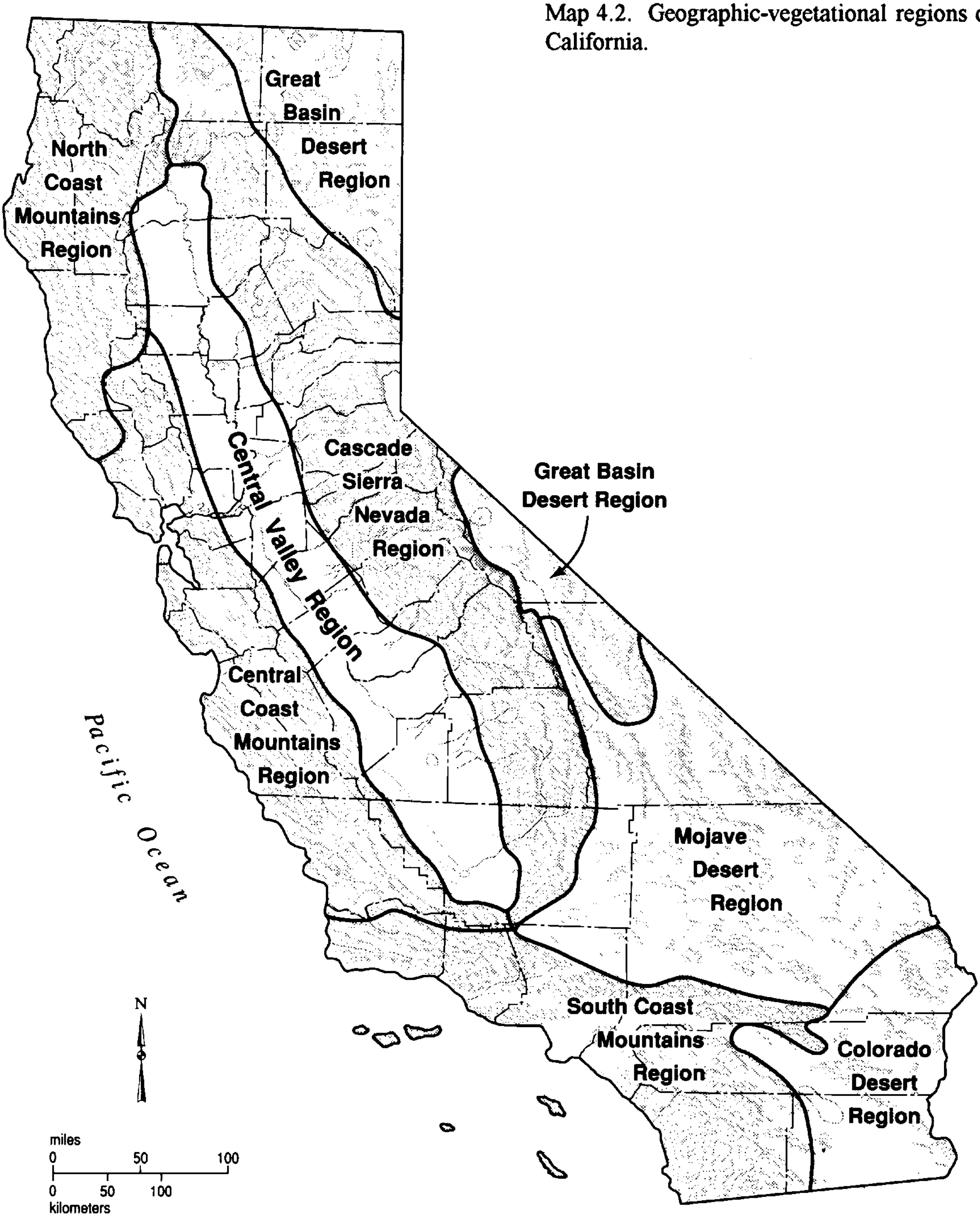
Geographic-vegetational regions of California

In describing the geography, climate, and vegetation of the state's eight geographic-vegetational regions (Map 4.2, p. 68), we rely heavily on Major (1977).

The **North Coast Mountains Region** (Klamath Mountains and part of the Northern Coast Ranges including the Siskyous) is a rugged coniferous-forest-covered land rising from the coast to heights exceeding 2,200 m. It receives the greatest annual precipitation of any area in California (278-440 cm). At the more coastal, lower elevations, temperatures are cool in summer and only slightly cooler during winter. Higher elevations may experience winter freeze.

The **Cascade-Sierra Nevada Region** (Cascade Range, Sierra Nevada), much of which is 2,750-4,250 m in elevation, separates the Central Valley from the deserts it has created in its rain shadow to the east. The term "rain shadow" reflects the fact that as weather systems rise up mountain ranges they cool and atmospheric moisture must be dropped, leaving little for the land "over the hill". So, on the windward western slopes of the range, precipitation increases with elevation but only to about 2,500 m; greater heights receive less moisture because little is left to fall, and of course the leeward eastern side receives less yet. Much of the precipitation falls in the form of snow, sometimes accumulating in drifts 20 m or more deep; and frost can occur on any day of the year (Williamson *et al.* 1986). These changing environmental conditions with elevation, and the differential adaptations of plants to them, help explain why Chaparral (a plant community dominated by low-growing woody shrubs with tough evergreen leaves), which is typical of the foothills, grades gradually into deciduous oak forest, then coniferous forest, and

Map 4.2. Geographic-vegetational regions of California.



finally into grass-amongst-rock, or nothing-but-rock, above tree line.

The **Great Basin Desert Region** (Modoc Plateau, Great Basin Desert) occupies the area east of the Sierra Nevada and Cascade Ranges in the extreme northeast and east-central parts of the state. Elevations are mainly 1,500-2,000 m, and precipitation ranges from about 10-50 cm. Most moisture comes in the cold winter, but the Region has more summer rain than do parts of California with a Mediterranean climate (areas where warm, dry summers and cool, wet winters are the norm). The climate of the Great Basin Desert favors sagebrush (*Artemisia tridentata*) and bunch grasses.

The **Central Valley Region**, varying in elevation from near sea level to about 300 m, lies in the rain-shadow of the Coast Ranges. Annual precipitation, reflecting this rain-shadow phenomenon as well as a north-to-south decrease in the frequency of storms, ranges from around 96 cm in the north to about 15 cm in the south. A Mediterranean climate is typical of this region. The yearly repetition of rain followed by drought, when combined with the Valley's fine soils, tells us why this region was once a vast grassland. Of course, for all intents and purposes, the Central Valley is presently clothed only with agricultural crops, houses, and asphalt; and even agriculture is losing out to urbanization in places.

The **Central Coast Mountains Region** (Southern Coast Ranges and part of the Northern Coast Ranges) comprises a series of mountains largely covered with Chaparral and grassland valleys, extending from about 80 km north of San Francisco to Santa Barbara County. The Pacific Ocean borders this region on the west, while the Central Valley bounds it on the east. Elevations from 500 to 1,000 m are common, and several peaks exceed 1,500 m. The climate is primarily Mediterranean; the annual rainfall ranges from about 27-90 cm.

The **South Coast Mountains Region** (Transverse and Peninsular Ranges) is similar in many respects to the Central Coast Mountains Region. However, it has stronger affinities with the desert, and at lower elevations the Chaparral is replaced by Coastal Sage Scrub, a community of more sparse, less woody, and often summer-deciduous plants. This region is also bounded by the Pacific Ocean on the west, but by deserts on the east. Much of the land within its borders is 500-2,000 m in elevation, but several peaks ringing the L. A. Basin exceed 3,000 m. The climate is largely Mediterranean, with annual precipitation at less than 32 cm.

The **Mojave Desert Region** is in many ways a transitional area between the colder, more northern Great Basin and the hotter, more southern Colorado Desert. In this and other hot deserts, creosote bush (*Larrea tridentata*) and a number of other sparsely distributed shrubs, like burro brush (*Ambrosia dumosa*), predominate. Although a number of isolated peaks occur in the Region, elevations are usually between 500-1,500 m. Annual precipitation, mostly occurring in winter, is generally more than 11 cm but less than 25 cm. Death Valley, while lying within this region, is ecologically quite different, with high temperatures more typical of the Colorado Desert and an annual precipitation of only 4-5 cm!

The **Colorado Desert Region** (a subdivision of the Sonoran Desert) is restricted to extreme southeastern California, being bordered by the Colorado River on one side and foothills west of the Salton Sea on the other. This desert is generally less than 500 m in elevation and includes the other area in California that lies below sea level. One might expect it to be hotter and drier than the more northerly Mojave and Great Basin deserts, and this stretch of land does not disappoint! Annual precipitation, its pattern highly irregular, is generally less than 11.5 cm, and much of this meager rainfall drops from summer storms originating in the Gulf of Mexico.

Habitat categories and their associated species of fairy shrimps

A discussion of conditions required by fairy shrimps could be approached in a number of ways. We feel that presenting information based on an alphabetical listing of species would lead to a random discussion of habitats, and "Dullsville", as they say! A regional approach would certainly be better, but given such varied topography at that level, we could probably not avoid a similar pitfall, and "Dullsville II" would be the result. We believe our purpose will best be served by describing what we know about habitat requirements of the various species that live within what we call **habitat categories**. Because these categories approximate the eight geographic-vegetational regions just described, and will be noted in the same sequential manner, a comparison can readily be made between the two.

Remember, we have placed our habitat categories (Table 4.1) into a continuum which generally grades from cold to warm, and low- to high-salinity waters. Although predicting whether a

Table 4.1. Habitat categories and their representative species

Habitat category	Representative species
Cold-water pools which are low in dissolved solids, predictable, and long-lived	*Eubranchipus bundyi, Eubranchipus oregonus, Eubranchipus serratus, Streptocephalus sealii*
Cold-water pools which are low to moderate in dissolved solids, predictable, and long-lived	*Branchinecta coloradensis, Branchinecta dissimilis*
Cool-water pools which are low to moderate in dissolved solids, moderately predictable, and long-lived	*Branchinecta coloradensis* (suggested two new species), *Branchinecta conservatio, Linderiella occidentalis, Linderiella santarosae*
Cool-water pools which are low to moderate in dissolved solids, less predictable, and short-lived	*Branchinecta lindahli, Branchinecta longiantenna, Branchinecta lynchi, Branchinecta sandiegonensis, Branchinecta* sp. (midvalley fairy shrimp)
Cold- and cool-water pools which are moderate to great in dissolved solids, predictable to less predictable, and long-lived	*Branchinecta mackini, Branchinecta gigas*
Warm-water pools which are low to moderate in dissolved solids, less predictable, and long-lived	*Streptocephalus woottoni*
Warm-water pools which are moderate in dissolved solids, less predictable, and short-lived	*Streptocephalus dorothae, Streptocephalus texanus, Thamnocephalus platyurus*
Cool-to warm-water pools which are great to impressive in dissolved solids, predictable, and temporary or permanent	*Branchinecta campestris, Artemia franciscana, Artemia monica*

pool will fill with water each season is a risky proposition, it is also true that, in California, the general continuum described also leads from more to less predictability of the presence of water as well as its duration.

Our organization leads us to begin with fairy shrimps requiring cold habitats, that is those in rather predictable pools occurring in or near areas of coniferous forest at high to moderate elevations in the North Coast Mountains, Sierra Nevada, and Great Basin Desert regions. Next come the low-elevation cool-weather species, most of which live in grassland pools in northern and central parts of the Central Valley where rainfall is moderate and reasonably predictable. Then we move south to species inhabiting more arid grass- and shrub-lands where rainfall is less in amount and predictability. Following the trend to greater aridity, we describe cold- and cool-weather forms that dwell in desert alkaline basins. Next come those that are found in desert waters of low alkalinity during warmer times of the year. In various regions of California, low rainfall, saline geology, and periods of high temperature produce salterns with a unique fauna. Because of their peculiarity they are our final consideration.

As for how cold "cold water" really is, or what the limits are for "moderate" amounts of dissolved solids and "low" pH, or where in the continuum of conditions "long-lived pools" might fall, we have set some limits so that when no information for California species is available, at least a reasonable "guesstimate" can be made of the conditions that actually prevail. By the way, the boundaries chosen (Table 4.2) have bases in the data presented by Eng, Belk, and Eriksen (1990).

Regarding water temperature we make two points. First, in California's northern and mountainous localities winter cold turns aquatic environments solid if water is present, and snow covers the landscape, sometimes in exceptional amounts. The species of fairy shrimps that live there are adapted to hatch as soon as snow melts and pool sediments thaw, that is at or near 0°C. Secondly, cold waters do warm with the season, and collections, along with temperature measurements, normally have been made later in the season when animals are partially, if not totally, developed, and during the warmth of the day. We must recognize, therefore, that elevated temperature readings, possibly those near maximal, are more likely to be the data we have to describe the thermal environment. For example, later-season events occasionally boost pool temperatures as high as 25°C for a brief afternoon period, but if they do, night-time cooling inevitably swings the temperature back into the neighborhood of 10-15°C (Daborn 1976; Eriksen unpubl.). Given these realities, "cold water" habitats are best con-

Table 4.2. Quantification of pool habitat categories for California's fairy shrimps

Environmental Measure	Quantification Range
cold water	0 - 15°C 0 - 10°C for hatching
cool water	5 - 25°C 5 - 20°C for hatching
warm water	17 - 35°C 17 - 30°C for hatching
low alkalinity	few - 100 ppm
moderate alkalinity	100 - 300 ppm
high alkalinity	300 - <10,000 ppm
impressive alkalinity	>10,000 ppm
low TDS	few - 300 ppm
moderate TDS	300 - 600 ppm
high TDS	600 - >175,000 ppm
low pH	4.8 -7.0
moderate pH	7.0 - 8.3
high pH	8.3 - 10.5
short-lived pool	<3 weeks
long-lived pool	>3 weeks

sidered as places where temperatures normally fall between 0-15°C, but where short-term highs of 20° or even 25°C may be recorded. Utilizing similar arguments, we also provide "typical" temperature ranges for our other habitat categories (Table 4. 2, p. 71).

Total Dissolved Solids or **TDS** (dissolved gases go unmeasured), sometimes also referred to as salinity, is a commonly-determined environmental measure because dissolved materials are not only the nutrition source for plants and ultimately animals, but also determine the osmotic conditions to which an organism must be adapted. When materials dissolve, they normally form charged particles (ions). Because charged particles can carry an electric current, measurement of the amount of current conducted can be recorded as **conductivity**, usually in µmhos, or alternatively as ppm of TDS. Because the µmho unit is foreign to most folks, we have chosen to convert such measurements to ppm TDS using a conversion factor of 0.65 (Lind 1979). Certain soils and rocks (e.g., limestone) dissolve comparatively readily resulting in high-TDS water; other soils and rocks (e.g., granite) dissolve only grudgingly yielding "soft" water with little dissolved material. Certain of the dissolved substances affect the constancy of the acid-base relationships within the aquatic environment. **Alkalinity** (mainly the total of bicarbonate, carbonate, and hydroxide ions), or the acid-combining ability of water, is the normal measure of the acid-base stability (buffer capacity) of an aquatic environment. In pools with "low TDS", alkalinity typically falls within the range of a few to perhaps 100 ppm. When waters are scantily buffered as these are, carbonic acid (from the solution of CO_2 in water) and organic acids (particularly tannic acids, tea-colored substances derived from plant materials) may overwhelm the buffering capacity and make the **pH** acidic, that is, below the neutral value of 7.0 (e.g., pH readings in the 5-6 range). Also typical of pools with little buffer is a considerable shift of pH over a daily cycle (e.g., 4.9-6.2, 6.8-8.6; Eriksen unpubl.) brought about by the often substantial fluctuation in CO_2 as it is produced in respiration and consumed in photosynthesis. Increasing TDS, whether due to evaporative concentration in a single pool or exhibited in a series of pools, normally is associated with increasing alkalinity and, therefore, with increasing buffer capacity; pH thus generally rises, sometimes considerably above neutral, and, as it does, demonstrates less and less change through a 24-hour cycle.

Pool **predictability** is a tough category to define, but a reasonable generality to which we can adhere is the further north and the greater the elevation in California, the more predictable the pool. The reverse, of course, follows. All of us are well aware that California is faced with years of drought erratically strewn over time. Even so, most pools at higher elevations faithfully form from the melting of whatever snow volume accumulated over an entire winter. However, when rain events are responsible for filling a basin, pools are less predictable because storms must be reasonably heavy and of some duration, or back-to-back. Such conditions certainly occur more frequently in northern California than they do further south, and, given rain-shadow effects, pool filling in the deserts is not only inconsistent but often problematic.

Pools that dot California's landscapes may be fleeting or permanent. However, those that are of interest to anostracans have certain defined periods of containing water which are specific to each species. Our classification of pool **duration** has as its basis the fact that some species of fairy shrimps have the genetic capability of completing their life cycle in less than three weeks (sometimes as little as 11 days), while others require a greater period than that (although temperature considerably affects the actual time to cyst production). Thus we define "short-lived pools" as those which exist for less than three weeks, while "long-lived" describes waters that endure from three weeks to perhaps as long as 6 months.

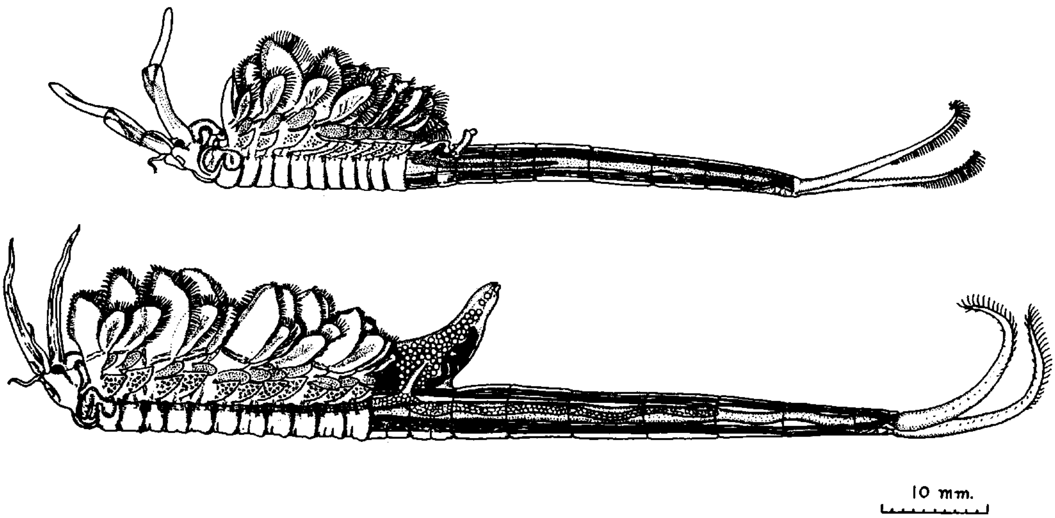


Fig. 4.1. Male (above) and female (below) of *Branchinecta gigas* from Lynch (1937); reprinted courtesy of the Smithsonian Institution Libraries.

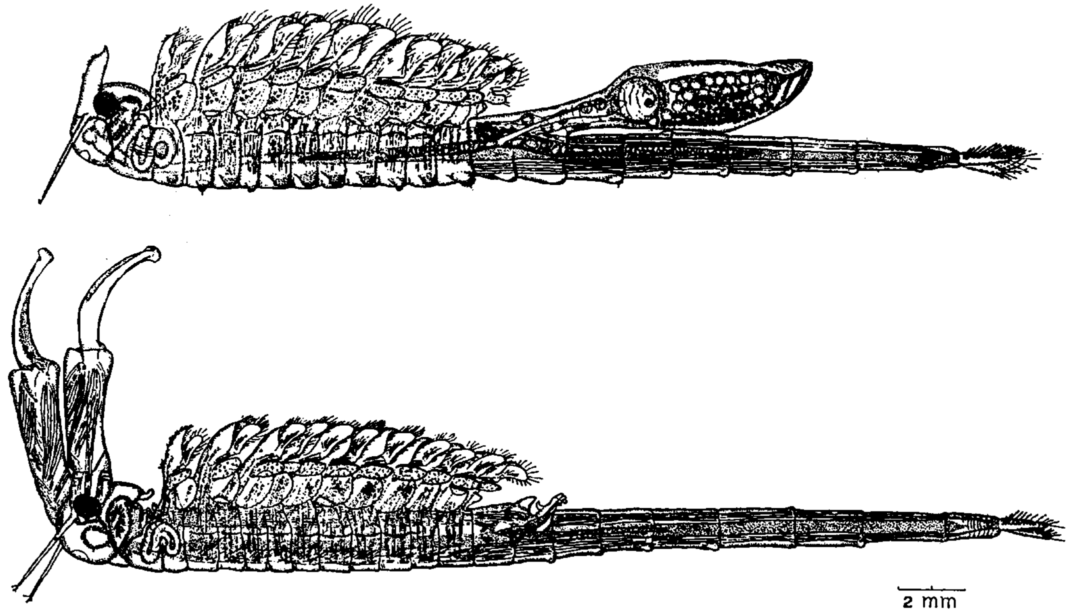


Fig. 5.1. Female (above) and male (below) of *Branchinecta campestris* from Lynch (1960); reprinted courtesy of the Smithsonian Institution Libraries.

Chapter 5

NATURAL HISTORY OF CALIFORNIA'S SPECIES OF FAIRY SHRIMPS

Much of what is known about the natural history of the anostracan fauna of our state was summarized in 1990 by Eng, Belk, and Eriksen. For some of the California species, little further information is available today than was at hand then, so the following discussions may take freely from our 1990 summaries; for their liberal use, we thank both Larry Eng and the *Journal of Crustacean Biology*! However, we do know a good deal more about where fairy shrimps occur, and to help you visualize those locations we have provided Maps 5.2-5.12 (pp. 118-128) which indicate pools or pool clusters supporting each species. To place these sites into the geo-political world of counties, and into the ecologically-meaningful geographic-vegetational regions of the state, refer to Map 5.1 (p. 117) and Map 4.2 (p. 68), respectively.

Information about California's fairy shrimps is unequally available for species and topic. For some, certain facets of their biology are totally unknown. Conditions under which data were collected in the field or experiments were conducted in the lab vary "all over the map", so in most cases it would be impossible to develop tables which present data in a comparative and summary manner. For these reasons, we have chosen to "spin a story" about each species, usually beginning with a unique feature of its life, then let the tale progress from there through what is known and what is surmised about its biology. In the process, we tell you what we can about each animal's **life history**, and use terms that have sometimes been applied with different meanings by different researchers. Our meanings are presented in the following sketch of the stages of a fairy shrimp's life. To begin with, suitable conditions are necessary to trigger **hatching**, an event that is normally completed within a few days of cysts being submerged in water. All individuals which emerge during this time are considered a **cohort**. If appropriate conditions recur, another hatch may yield another cohort to swim with the first. Hatching produces a larva which develops through juvenile stages to a **sexually mature adult**, recognized by the possession of one or more cysts in the female's ovisac. A batch of cysts in the ovisac is referred to as a **clutch**. Some species generate only one clutch during their life; others can produce clutch after clutch until they die. A female's **fecundity** is measured by the total number of cysts manufactured over her lifetime. The length of that lifetime (birth to death) is referred to as **longevity**.

As a final consideration before we discuss the natural history of California's fairy shrimps, you have undoubtedly noted that temperature has arisen repeatedly as an environmental measure of great consequence to the differential distribution of fairy shrimps. Among other things, cysts hatch only within a certain temperature range for each species; metabolic rate, and thus rapidity of growth to sexual maturity, are also sensitive to temperature, and are species-specific. Finally, the number of cysts per clutch seems directly related to temperature, while the size of cysts, as well as the size of newly hatched larvae, appear to be inversely related to the temperature to which the species is adapted. That is, fairy shrimps of cold water make fewer but larger cysts, and thus larvae. We explain this by example. When we averaged all of Belk's (1977b) data relating to 19-20 mm-long females, the following picture emerged: rainpool anostracans produced 547 cysts measuring 0.26 mm in diameter, and larvae 0.36 mm in length at hatching. By comparison, individuals from snow-melt pools came forth with 98 cysts of 0.35 mm diameter that resulted in larvae 0.62 mm long. Striking differences, but the adaptive rationale? This is Denton's work, so let's quote what he has to say: "...production of small eggs...maximizes the number of offspring in a (less predictable) food-rich pond, and the generation of larger eggs...increases the survival chances of each larva in a food-poor (predictable) melt pond." (Belk 1977b). More recently Mura (1991c) has corroborated, with Italian anostracans, the relationship of increasing cyst mass with increasing elevation of the populations that produce them. However, she offers the important caveat that because of the intraspecific variation now on record, an average cyst size is not meaningful and, therefore, such a measure can no longer be considered a valid species trait. Still, as information of general comparative value, you will find cyst measurements reported as we busy ourselves exposing available details about the wonderful lives of California's fairy shrimps!

Fairy shrimps of cold-water pools which are low in dissolved solids, predictable, and long-lived

In California, predictable pools containing cold water are found in the North Coast Mountains and Cascade-Sierra Nevada Mountains regions. Here, basins usually fill by snow-melt to yield waters that are typically "crystal clear", although possibly tea-colored. We know essentially nothing about the chemistry of these places, but if they are like the smattering of pools in similar western regions about which we have some information, we would expect somewhat acidic waters very low in alkalinity and TDS.

Our stories about the fairy shrimps that are restricted to these mountainous habitats begin with California's three species of *Eubranchipus* and one of the state's streptocephalids, *Streptocephalus sealii*. The *Eubranchipus* species are known only from 1,250-1,650 m in elevation where they stake their claims in meadow pools surrounded by coniferous forest. At somewhat higher altitudes (mainly 2,000-3,000 m), and within the heart of the coniferous forest, lie the vast majority of known residences of *Streptocephalus sealii*.

Eubranchipus bundyi

(Map 5.2, p. 118)

Eubranchipus bundyi is well known for dwelling in pools scattered along the northern states and into Canada, even Alaska. But does California possess habitat conditions suitable enough to support this creature? That intrepid field man Christopher Rogers answered this question in the early spring of 1990 (May 8) when he brought forth the first California collection of *Eubranchipus bundyi* from a 30-cm deep portion of Grass Lake in Siskiyou County. Now this far-northern California jurisdiction covers a large piece of variable terrain, so where, pray tell, is Grass Lake, and what kind of a place is it? Well, it lies along U.S. Highway 97 between the coniferous forest slopes of Goosenest and Deer Mountains of the Klamath National Forest, 35 km northeast of the town of Weed. Rogers (1996) notes that the lake is seasonally astatic, covers about 3 km^2, has a maximum depth of 0.5 m, and lies at an altitude of 1,535 m. The basin is largely covered with sedges and perennial grasses (hence its name???), and receives water from snow-melt.

How *E. bundyi* got to Grass Lake is conjectural, because not only did Coopey's (1946) collection of branchiopods from southeastern Oregon, including the Cascades, not reveal this species, but the closest known populations are in the Uinta Mountains of Utah and Medicine Bow Mountains of Wyoming at elevations exceeding 3,000 m, and on the Kaibab Plateau of Arizona where altitudes range from 2,100-2,700 m.

Eubranchipus bundyi is best known from pools in non-montane coniferous and deciduous woodlands (e.g., Broch 1965; Dexter 1953, 1967) but has also been taken in tundra, flood-plain, swamp, prairie sandhill, and high-desert salt-bush sites. Most of these habitats suggest clear water of very low TDS, alkalinity, and pH. However, the only data recorded when fairy shrimps plied the pools come from four sites that appear to span habitat types: alpine, mixed deciduous woodland, prairie, and high-desert. In these places alkalinity ranged from 1-513 ppm, pH from 6.9-9.0, and turbidity from clear to opaque (Daborn & Clifford 1974; Horne 1967; Maynard 1977; McCarraher 1970). The higher values all come from Nebraska's sandhills and seem atypical of its more common sanctuaries, although Chelberg (1973) affirms *E. bundyi* does reside in hard-water pools on limestone soils of Minnesota's prairie counties .

Where California's Grass Lake population straddles the known chemical range for the species is uncertain. In his article documenting *E. bundyi* in Grass Lake, Rogers (1996) reports some unpublished data collected by the California Department of Water Resources in the 1950s and averaged for all annual lakes in the Shasta Valley. The data (showing very high levels of Na^+, Cl^-, aluminum, boron, and pH), if true for Grass Lake, and we believe they are not at least in early season when fairy shrimps are in residence, suggest the place is a strange water-hole indeed. Strange too is that surrounding soils contain "high amounts of granite and lava rock", geological types which should yield soft water as did soils of the same description in northeastern Minnesota (Chelberg 1973). Before we admit this odd chemical soup is the actual liquid in which *Eubranchipus bundyi* swims, we would wish for analyses soon after snow-melt fills Grass Lake and individuals hatch and ply its icy waters. Richard Hill took such samples on 10 May 1995 and recorded a pH of 6.5 and a TDS (from conductivity) of 91 ppm, values more in line with what we would expect. However, Richard was unsure about the calibration of his meters, so more data are necessary to determine what kind of a chemical habitat Grass Lake really is.

Broch (1965), Daborn (1976), and Maynard (1977), studying pools full of these creatures near Ithaca, New York, Edmonton, Alberta, Canada, and Salt Lake City, Utah, respectively, observed that metanauplii averaging 0.69 mm in length hatched as soon as bottom sediments thawed in spring. Belk (1977a) confirmed the latter observation by experimentally showing that larvae from a population on the Mogollon Plateau of Arizona emerged well at 5°, poorly at 10°, and not at all at 15°C. Maynard (1977) observed that maximum longevity of her animals was 40 days, while Daborn (1976) counted 41 for males and 44 for females although most lived only 30-35 days. Broch described females dying at 49 days after producing but one clutch of cysts. Daborn (1976) and Maynard (1977) agreed that only one clutch (averaging 22 and 21 cysts, respectively) is normally produced before death, although a few females may turn out a second clutch with a greater number of cysts (a situation perhaps verified by data from Linder 1959). In some of Daborn's females, eggs that ultimately became cysts began to appear in the brood pouch at 10 days, and, after 20 days, 70% of females carried them. However, Maynard's individuals were probably cold-inhibited, for they did not begin to reproduce until 28 days after hatching.

Showing that published observations and pronouncements are not always the final word, Denton, the eager graduate student that he was at the time, counted 78 cysts crammed into the brood pouch of a female *E. bundyi* from Arizona. This number is 3.5 times the totals recorded above. Even so, 78 cysts are not that many when compared with the 846 he removed from a female *Streptocephalus dorothae* (Belk 1977b). Maynard (1977) determined that the average cyst size for her Utah shrimps was 0.36 mm, but Denton's Arizona animals could only manufacture cysts averaging 0.34 mm in diameter, while those from California came in with a comparatively wimpy 0.31 mm average (Hill & Shepard in press).

In contrast to *E. bundyi*'s 7-week maximal longevity in the field, would you believe 20 weeks in the laboratory? Yes, Chelberg (1964) pushed life-span that far by maintaining some Minnesota shrimps at their hatching temperatures of 1-2°C; and no, such conditions are not realized in nature. By contrast, when *E. bundyi* is warmed too much, that is to a constant 25°C, more than 50% of them succumb (Belk 1977a). Similarly, young larvae which survived only 2-3 days when subjected to 22-23°C, grew to maturity when maintained on a fluctuating regimen of 16 hours at 2°C, then 8 hours at 22-23°C (Chelberg 1964). These latter data support our earlier statement that cold-water fairy shrimps, though occasionally collected during the day in waters as warm as 25°C, do not face those conditions for long because they live in areas where temperatures drop drastically at night.

As seems typical of fairy shrimps from predictable pools, *Eubranchipus bundyi* seldom occurs with other anostracans. When that does happen, *E. bundyi* does not share equally; it either numerically dominates or shows up as a small fraction of the total fairy shrimp population. In California's Grass Lake, Christopher Rogers netted it swimming alone.

Eubranchipus oregonus

(Map 5.2, p. 118)

Our mention of the town of Weed calls to mind the first known locality for *Eubranchipus oregonus* in California. Ken Beatty of the College of the Siskiyous sent us his collection of 28 February 1986 from a pool south of town which is situated at approximately 1,250 m elevation. You note we said that this was the first "known locality". Actually, the U.S. National Museum of Natural History holds a collection made in February 1956 by F. Flammer, taken from an "ephemeral pool south of Brocot, California". We have pored over maps, even made a name search, but can locate no such place. So, if any of our readers can direct us to the elusive Brocot, perhaps we can better follow the route of this fairy shrimp into California.

Actually, its approximate route is probably not all that secret. Coopey (1950) believes the species has a general distribution in the valleys of western Washington and Oregon, for he collected it as far south as Cottage Grove, Oregon, some 200 km as the duck flies north of the California border. We are of the opinion that "Brocot" would be an interesting place to locate and fit into the dispersal path of *E. oregonus*, for Brian Quelvog established (27 March 1995) that this species resides in Abernathy Meadows (1,350 m in elevation), immediately north of Yosemite National Park in Tuolumne County. More recent yet, a collection of this beast was taken near Schoettgen Pass at 1,450 m, some 35 km to the northwest, in a snowmelt, silty-bottomed, meter-deep pool. These locations place the species 415 and 450 km by air southeast of the Weed population.

Knowing if and where any stepping-stone pools are located along the Cascade-Sierra chain became an interesting challenge for CalTrans biologist Richard Hill. Perhaps the phantom locality of "Brocot" lies between Weed and Abernathy Meadows, he reasoned, so maps were scrutinized and a creative possibility emerged. West of Lassen National Park lies the village of Viola in Shasta County. Departing southeast from Viola is Broke Off Meadows Road which traverses country from 1,500-2,000 m in elevation, and southeast of road's end is Brokeoff Mountain (yes, different spellings). Given the seemingly appropriate elevation, and that the meadows are on a straight-line flight path between the known sites, maybe, just maybe, Richard found the phonetically-misunderstood "Brocot".

Bird flight paths are not all straight lines however. Nor do all of our feathered friends fly along the Cascade-Sierra chain. Obviously waters of the Central Valley and lagoons along the coast are some of their favored resting and feeding grounds. Perhaps cysts of *E. oregonus* were transported along their coastal trade-routes from Oregon to California, for almost 7 km south-east of the twin cities of Rio Dell and Scotia, in the valley of the Eel River, supposedly lies a pool, its nature undescribed, from the bowels of which our subject is said to have been seined. We have the collection, but if from a pool in this area we have a unique find, so unique that several expeditions (unsuccessful) have been mounted to confirm it. And why is it unique? Not only would this be just the fourth known location for the species in California, but it would be one of **only four anostracan sites in the North Coast Mountains Region** (Map 4.2, p. 68). One could assume fairy shrimps are not common in these wet climes, so until someone is led knee-deep into this otherwise unknown pool we consider the record anecdotal. With Brocot not forgotten, we recently learned that also in this general area and immediately to the east of Arcata Bay is a spot on the map labeled Bracut. Could **this** be the elusive "Brocot"? And does *E. oregonus* live in its vicinity?

The *Eubranchipus oregonus* site near Weed is seasonally astatic and does not form every year. When it does fill, snow-melt provides the water, usually in February, and it lasts through April. The pool is held by deep clays in a natural drainage under a railroad span which crosses a wet meadow surrounded by coniferous forest. At maximum the basin is about 8x3x0.2 m and holds clear water with poor buffering capacity (Beatty pers. comm.). Being a biology professor in Weed, Beatty describes these conditions from many seasons of observation. However, on 10 May 1995, Richard Hill found a "huge pool", at least a football field long and 10-12 m wide, backed up along the railroad bed. Although unable to wade to its center, he netted *E. oregonus* in areas where his boots were safe from filling. The clear water had a pH of 6.5 and a TDS (from conductivity) of 91 ppm, corroborating Ken Beatty's verbal description of conditions.

In Abernathy Meadow, which is also surrounded by coniferous forest, a "spring pothole" in granitic soils houses *E. oregonus* (Hill, pers. comm.). Whether or not water remains in the basin when winter arrives is unknown, but if it does, certainly it freezes. And whether the pool is filled mainly by snow melt or by the spring is also unclear. What we do know is that in the spring of 1996, when the site was brimming with fairy shrimps, the clear water was 11°C and had an alkalinity of 68 ppm (Hill again). These conditions are not at odds with what Coopey (1950) felt was characteristic habitat of *E. oregonus* in western Washington and Oregon. He described a site near Seattle, Washington, as a "temporary, *Typha* bordered pond" with a maximum depth of 1.3 m that contained much detritus and "yellow to brown stained water". It filled in late November and was dry by late June or July. During his studies, temperatures were 1°C (under ice) to 16°C, and the water was mildly acid (pH 5.8-6.2) .

Coopey's work also demonstrated that cysts (0.35 mm in diameter; Hill & Shepard in press) began to hatch three days after pool-filling; and though the process continued for 5 weeks, 75% of the metanauplii appeared within the first 10 days. Although hatching occurred at temperatures of 4-9 °C, water of 10-15°C was required to bring females to maturity. At maximum female size, ovisacs commonly possessed 150-250 cysts. Coopey watched females doing their reproductive thing until temperatures reached 26.5°C. Armed with this information on clutch size and longevity, he estimated a female's fecundity at 300-400 cysts. Apparently a good deal of this production was accomplished without pestering males, who had succumbed when temperatures attained only 16.5°C. Whether thermal limits were surpassed, or the sexes merely lived out their genetically allotted time, is not known. In any event, female longevity of 23-25 weeks appears to be one of the longest for North American Anostraca.

Eubranchipus serratus

(Map 5.2, p. 118; back cover)

Eubranchipus serratus, reported by Eng *et al.* (1990) as known only from McCoy Flat, 6 km west of Eagle Lake in Lassen County, has now been collected by Richard Hill and Christopher Rogers from additional sites in the same general region. Pools in this Cascade Range area lie at elevations from 1,500-1,750 m in small meadows surrounded by heavily logged coniferous forest which, immediately east of Eagle Lake, grades into Great Basin Desert. About 120 km north is California's border with Oregon, and about 20 km into Oregon is a pool identified by Coopey (1946) as containing *E. serratus*. Because this species spans the continent, with the U.S.-Canadian border being about its northern limit, dispersal routes along the Cascades from British Columbia through Oregon and into California were undoubtedly used to establish the populations in Lassen and Shasta counties. Although there are more southern populations in Virginia, Oklahoma, and Arizona, we consider it unlikely, given intervening habitats, that *E. serratus* arrived in California from the south and worked its way north along the Sierra and into the Cascades.

Information from California specific to this species is pretty much limited to the knowledge that it occurs where winter freeze is long and hard. However, in early October of 1995, Clyde ventured forth to find the McCoy Flat site in order to determine if it was anything like the Montana, mountain-meadow pools where, for a number of summers, he had pursued *E. serratus*, and in turn had been pursued by mosquitoes. Results were positive in all aspects, including mosquitoes. Here was a partially mud-bottomed basin, still holding clear water (1995 was wet!), and, although lacking fairy shrimps, was replete with *Carex*, *Juncus*, and *Ranunculus*, filled with the typical later-season menagerie of aquatic insects and frogs (*Hyla*), and surrounded by cow dung, aspen, and conifers, in that order of proximity.

Of the two dozen or so California collections, only the one from McCoy Flat was made in fall (early December). This probably means the pool was filled by rain, although if 1995 is any indication, the possibility exists that water remained year-long, and in the fall became cold enough to stimulate hatching but remained liquid long enough to allow development before winter solidified the habitat.

Studies outside California (Belk 1977a; Coopey 1946; Dexter & Ferguson 1943; Prophet 1963a; Eriksen unpubl.) indicate that *E. serratus* is typical of seasonally astatic waters in forests, meadows, and grasslands that are subject to winter freezing. Autumn, winter, and spring collections have been reported at water temperatures usually between 1-17°C. In one instance the surface of a pool reached 23.5°C, but near its bottom the water was a cool 15.1°C; it is doubtful that individuals experienced the surface temperature, for *E. serratus* is known to congregate in and around vegetation and to swim removed from the surface, perhaps selecting cooler water in such places. We say this because McGinnis (1911) showed shrimps select temperatures of 15-17° C, will not voluntarily swim into water over 17°, and die at 28°C. Belk (1977a) was able to acclimate adults at 25°C for 24 hours, but 50% of them succumbed within an hour when transferred to 31°C. Given such information, the fact that fairy-shrimpologist Richard Hill found *E. serratus* in a number of pools around Poison Lake (Lassen County) at temperatures from 21-24°C should not raise too many eyebrows. However, he also saw "huge numbers...in a cut off pool adjacent to the lake" at 26.8°C, which suggests that either this population might soon be terminated by elevated thermal conditions, or such daytime highs were only fleeting because of substantial nighttime cooling, or colder bottom water was available. Place a check opposite your favorite hypothesis!

Although pools inhabited by *Eubranchipus serratus* are usually at least partially mud-bottomed, they also possess significant amounts of living and dead vegetation and thus contain clear, though often tea-colored, water. The result is very low TDS, poor buffer capacity (low alkalinity), and a slightly acidic pH, although values from 4.9-8.2 are on record.

Cysts of *E. serratus* will not hatch at 20°C, do so poorly at 15°C, but yield larvae well at 5-10°C (Belk 1977a; Prophet 1963b). 0°C must also be suitable because Dexter and Ferguson (1943) reported metanauplii swimming amongst flooded ice as their pool began to thaw, and development continued for several weeks under heavy ice cover. As is typical, length of the life cycle, and time to maturity, depend on temperature. For example, individuals have been known to survive almost 9 weeks, reaching sexual maturity after 5, under "moderate temperature conditions" (Dexter & Ferguson 1943). But Coopey (1946) noted that individuals subjected to what he supposed were cooler than average temperatures did not reach maturity until 6-8 weeks had passed, and lived a total of 11.5 weeks. In his Kansas lab, and at a constant 15°C culture temperature, Prophet (1963b) noted that a female's ovaries began producing eggs about day 13. Over a life span, the average female made 366 cysts, but the variability (42-640) was considerable, as was the number per clutch. Prophet's recorded range of 1-290 comfortably encompasses the 157 cysts counted by Denton in a 22.8-mm Arizona female (Belk 1977b). As is typical of species living in snow-melt pools, cysts were large (average 0.37 mm), in fact the largest of those Denton measured in his study. This did not surprise Hill and Shepard (1997) who found cysts of *E. serratus* to be the largest (0.39 mm) among California Anostraca (except for the giant fairy shrimp). Also contained in Denton's study was the fact that larvae of *E. serratus* hatch as big metanauplii (0.58-0.73 mm), as do other snow-melt pool species.

Although both Christopher Rogers and Richard Hill have found *Branchinecta coloradensis* in several pools containing *E. serratus* in the vicinity of Poison Lake in Lassen County, the latter far outnumbered the former. Because it seldom has been collected with other anostracans elsewhere, *E. serratus* seems to follow the pattern of cold-water fairy shrimps being "loners".

Streptocephalus sealii

(Map 5.3, p. 119)

This often strikingly-colored species occurs in a number of sites in California. All but two are within the coniferous forest belt of the moderately high, glaciated, Cascade-Sierra Nevada Mountains Region, from Siskiyou County at the California-Oregon border to just south of the Mammoth Lakes area, barely into Inyo County, somewhat over 500 km to the south-southeast. The two exceptions to this distribution are located in the Siskiyou Mountains of the North Coast Mountains Region some 200 km west of the northernmost Cascade-Sierra sites. A pool near Sanger Lake, about 7 km south of the Oregon border in Del Norte County, appears typical of those occupied by other populations of *Streptocephalus sealii* in that it is rock-strewn, mud-bottomed, filled with clear water, and rests in a small meadow surrounded by coniferous forest and guarded by Steller's jays. Another 40 km due south, and barely east of the mountain crest that separates Del Norte County from this Siskiyou County location, lies a truly remote and undescribed *S. sealii* hideout. These pools are of note because they harbor two of the three proven anostracan populations in the North Coast Mountains Region. Additionally, at elevations of almost 1,600 m, these and the two sites in eastern Siskiyou County at 1,200-1,400 are the lone locales in California where *S. sealii* has been documented below 2,000 m, although more will undoubtedly be discovered, most probably in this general region. Populations of *Streptocephalus sealii* in the Cascade-Sierra Nevada Region are typically at elevations from 2,100-2,500 m, although several lie at 2,770, 3,032 (Tioga Pass in Yosemite National Park) and 3,219 m (the only known Inyo County site).

In California, this species has been netted from late June to mid-September – with one exception, that being an interesting and historical one! A collection, given credit as the first record of the species in California, was made "March of 1930 in the High Sierra Mountains". A local placement of this population is obviously impossible, but a low-elevation site in the high Sierra, though a contradiction of terms, may be responsible for the much earlier collection date.

Information concerning the California habitat of *S. sealii* is all but absent. What little we know from recorded data shows it swims in waters from 10.6° (and certainly much lower) to 23.4°C in seasonally astatic, perennially astatic, and aestival pools where winter snows lie deep. The most common habitat is a meadow basin surrounded by coniferous forest, and strewn with granite outcrops or boulders, and often fallen trees. Such pools are glacially formed, probably kettle holes, mud-bottomed, and have clear, though often tea-colored water because of dissolved organic matter leached from meadow grasses or conifer needles. The perennially astatic waters are a small crater lake, a cirque lake, and several 1-2 m-deep glacial basins covering 987-8,195 m^2, at elevations around 3,200 m (Jim Muck pers. comm.).

These general habitat conditions suggest slightly acidic, soft-water of low buffering capacity. The only data from California support such generalities and come from the perennially astatic Lower Inyo Crater Lake in Inyo County. This unique-sounding habitat is lightly turbid from volcanic clays derived from pumice, has very low buffering capacity (20-40 ppm alkalinity), and a pH of 6.8-7.1 during the time shrimps and Clyde were present together (Eriksen *et al.* 1988b).

Outside California, *S. sealii* has been dipped from clear, snow-melt pools in high mountains as well as from low-elevation "mud holes", turbid cattle-watering sites, and summer-rain-filled, tea-colored, forest waters. Charted temperatures range from 0.5-35°C (one record of 42°C) in waters of low to moderate alkalinity and conductivity, and a corresponding pH variation of 4.9-8.7.

This species is the most widely distributed fairy shrimp in North America, occurring from southern Canada to Mexico's southern most state, and from coast to coast across the U.S. Such a distribution involving a wide diversity of habitats would require a fantastically labile physiology. We wonder if it is not more reasonable to think of this anostracan as being at least two, if not more, sibling (cryptic) species. We say this because, first, the high mountain pools of Arizona and California, fed by snow-melt, are quite different from plains and bayou basins to the east and south which fill by rain. Second, different hatching mechanisms are indicated in those contrasting conditions. Cysts of "lowland" *S. sealii* are said to release nauplii only from 10-32°C (Moore 1963; Prophet 1963b). Cysts of plateau and mountain populations presumably hatch in snow-melt waters. But Denton, who had no trouble coaxing nauplii from Louisiana cysts, had no luck hatching high-elevation ones from Arizona, nor was Richard Hill's brief attempt successful with cysts from several Sierra populations.

Although Denton's search for a reason that might explain the dichotomy in laboratory hatching success between high- and low-elevation populations of *S. sealii* was unsuccessful, he did discover some significant reproductive differences between the two (Belk 1977b). For example, he noted that Arizona animals possessed significantly larger cysts (0.34 vs. 0.24 mm in diameter) which contained embryos more than twice the volume of those from low-elevations, and consequentially the high-altitude *S. sealii* produced fewer cysts per clutch on a size for size basis. To illustrate, the largest Louisiana female had 315 cysts in her ovisac; she was 19.4 mm long. By comparison, a slightly larger Arizona female (23.0 mm), the high-altitude specimen closest in size with a filled ovisac, bore only 86 cysts. Strikingly, the largest Arizona female (34% longer than her biggest lowland counter part), possessed 22% fewer cysts (only 246). With interest whetted, Belk *et al.* (1990) did a follow-up study with other low-land populations and some from the high Sierra. Although this time the average size of cysts of lowland forms was 0.26 mm, mountain cysts continued to average almost 0.34 mm, with none smaller than 0.31 mm. The hypothesis seemed confirmed! Or was it?

As scientists, we generate ideas freely from data at hand. However, not uncommonly, some of those data seem at odds with what we think we know and thus cry out for resolution. A case in point is some measurements sent to us by Hill and Shepard (1997). Their cysts of *S. sealii* from the Sierra had a composite average diameter of 0.27 mm, obviously a size more reminiscent of those from low-elevation rainpool animals, but their diameters ranged from 0.24-0.31 mm. That the mass of cysts is considerably more variable among populations than was previously imagined is undeniable. Still, we wonder if any of the Hill and Shepard samples came from populations with which Denton dealt? Did they come from animals living at comparatively low elevations? Are the differences recorded really the result of variation between populations, or are sample sizes for any of the studies large enough to establish a meaningful average? What we all know is that the hypothesized relationship originally conceived by Denton (pp. 75-76) requires that additional inquiring minds probe its ramifications and possible exceptions.

Before we leave these data on cyst, clutch, and larval size, there are several more comparisons to consider, and, you guessed it, more questions to ask. Anderson (1984), knowing that a single female *S. sealii* from low elevations can produce multiple clutches, estimated that, if this normally long-lived creature survived three months, her fecundity could top 1,500 cysts. Prophet (1963b) had already proved such an estimate reasonable, for one of his lab-reared females actually manufactured 1,791 cysts!

Are such levels of fecundity attainable by *S. sealii* populations residing in western mountains, or are reproductive characteristics of the latter more like those of other high-elevation, snow-melt pool species we have already considered? Well, for starters, larvae of mountain *S. sealii* emerge from relatively large cysts to swim in melt-water-filled basins. Are these larvae released as metanauplii as with other high-elevation species possessing large cysts, or do nauplii pop out as in rainpool forms of *S. sealii*? No one knows. And how long do high-elevation animals live? How many clutches can they generate in a season – one, as do other snow-melt pool species, or from 3-14 as per low-elevation forms (Prophet 1963b)? If more, what is their maximum fecundity? Ah, questions, but few answers. At least we know their clutch size is relatively small!

We also know that the temperature tolerances of adults differ. Belk (1977a) recorded a one-hour LD/50 (a comparative lab measure of the temperature at which 50% of the experimental organisms survive and 50% die within one hour) of 38°C for mountain populations in Arizona, while Moore (1955) reported 44.5°C for animals from Louisiana. Moore also noted that several hours at 42°C was lethal for bayou beasts, as was 40°C, but only after 18 hours of exposure. Finally, Moore showed that "warm-water" (low-elevation) *S. sealii* could not be acclimated to cold water, being sluggish even at 7-8°C. Given conditions in which California individuals swim, we assume they are physiologically like *S. sealii* from the mountains of Arizona and unlike their low-land counterparts.

Streptocephalus sealii, which has not been observed in California coexisting with other anostracan species, is yet one more example of a cold-water, predictable-pool fairy shrimp which swims alone.

Fairy shrimps of cold-water pools which are low to moderate in dissolved solids, predictable, and long-lived

Branchinecta coloradensis

(Map 5.4, p. 120; Fig. 5.2, below)

Branchinecta coloradensis, named in 1874 for its collection site in the Colorado Rocky Mountains, conjures up thoughts of high terrain and snow-melt pools embracing crystal waters. We might think of it as the stereotypical organism of such places, for this species has been taken from 2,900-3,530 m in mountains of a number of western states, including California. Our four known high-elevation sites, 15 km from each other on either side of the Sierra crest in Inyo and Fresno counties, lie at 3,150-3,530 m. The problem with thinking of this fairy shrimp as a resident only of mountains is that what we presently call *B. coloradensis* also appears in some prairie pools in Oklahoma, Wyoming, Alberta, and Saskatchewan, and it frequents high deserts throughout the West, including those in Oregon and California. A number of havens for this animal are scattered along a 100-km stretch of Great Basin Desert, 1,300-1,600 m in elevation, between Alturas and Susanville in Modoc and Lassen counties. Westward toward the Sierra-Cascades, and on the Modoc Plateau of Lassen County, *B. coloradensis* inhabits meadow pools down to around 1,000 m (Christopher Rogers, Richard Hill, pers. comms.).

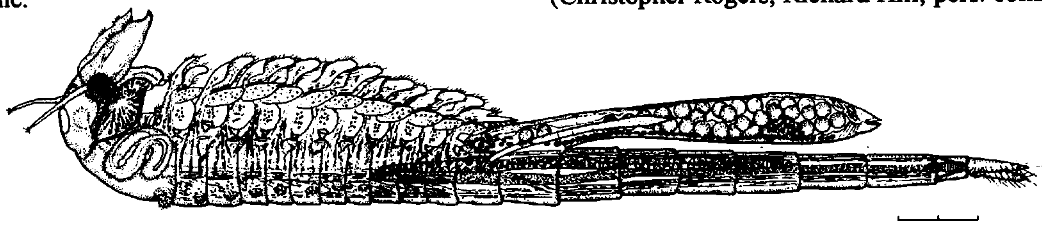


Fig. 5.2. Female of *Branchinecta coloradensis* from Lynch (1964); reprinted courtesy of *The American Midland Naturalist* (scale = 2 mm).

Its crystal-clear Sierra haunts, with surface areas from 49-355 m^2 (Jim Muck pers. comm.), are of glacial origin; many localities in the high desert are road-side and railway-side ditches holding turbid water; and those in forest meadows are largely clear-water basins whose dimensions and origins are unknown but which commonly lie on soils of volcanic origin. Whatever the site, most of these waters are seasonally astatic, a few aestival, and all are filled initially by snow-melt.

Because its habitats seem so environmentally different, the obvious question is: what traits do these places share that *Branchinecta coloradensis* requires? Freezing winters and a pulse of water of very low osmotic concentration from melting snow appear to be the obvious factors. Simple, right? **Perhaps wrong,** for *B. coloradensis* has popped up in several California habitats which look quite different from those described so far. One, Panamint Dry Lake, occupies a 475-m-high basin one valley west of Death Valley. "Dry lakes", or playas, are usually quite alkaline, and the fact that the alkali fairy shrimp *B. mackini* dwells here as well is living proof of the conditions in this habitat. Interestingly, when Clyde dipped into the turbid and alkaline water of Panamint Dry Lake during the plentiful rain-year of 1995, *B. coloradensis* was conspicuous by its absence, only *B. mackini* graced his net. Obviously conditions here aren't always just right for the Colorado fairy shrimp.

Although the Panamint Dry Lake area may prove cold enough during most winters to satisfy what was thought to be a hatching requirement for the species, there are three other known sites containing *Branchinecta coloradensis* that do not normally receive intense cold, all in the Central Valley. These include a very large, turbid vernal pool, 70 m in elevation and about 15 km from the Sierra foothills, which lies east of Hickman in Stanislaus County. A second site is on the Sacramento NWR in Glenn County at its border with Colusa County. Joe Silviera, wildlife biologist at the Refuge, collected *B. coloradensis* early in 1993, and again in 1994, though not in 1995, in a pool he described as being turbid and alkaline, and 50 m in elevation. The most recent find, a collection taken in March of 1996 from an undescribed site a few km south of Colusa, was given to Christopher Rogers by William Beckon. If our Colorado fairy shrimp requires water the temperature of snow-melt as a hatching stimulus, this implies that a relatively harsh cold-snap settles in on these otherwise cool pools often enough to stimulate hatching and thus maintain their populations.

Richard Hill told us of transferring some *B. coloradensis* to his Sacramento lab from a site 1,700 m in elevation on the Modoc Plateau. His animals, kept at 10°C, went about their reproductive business and ejected many cysts into their aquarium habitat. Of course biologists are prone to experiment, and Richard observed that every time he lowered the temperature to around 5°C, presto, many of the cysts hatched. Drying was not required! Whether this scenario fits the "low-lander" populations we do not know. Lab experiments and continuous measurements of pool temperatures are called for to find out.

A hypothesis has recently been developed to explain the occurrence of this fairy shrimp in such diverse environments, and here it is for your consideration. Perhaps, in a situation analogous to that seen in *Streptocephalus sealii*, we are dealing with populations which developed from *B. coloradensis* cysts that were deposited in what at the time were atypical environments. Then because some individuals in these founding populations successfully adapted to the new conditions, they started down the ever-diverging path toward new species status. This idea is not without accumulating evidence. Intrigued by the problem, Christopher Rogers set about to study the morphology of these different populations in some detail. On the basis of preliminary observations, he felt that what we now call *B. coloradensis* may actually be a complex of three species, one from high mountains, one from the Great Plains and Great Basin Desert (including Panamint Dry Lake), and one from the Central Valley of California.

As we go to press, Christopher's hypothesis is having problems with variability in several taxonomic characters, both within and among populations. Help might come from protein analyses (electrophoretic studies), comparison of cyst sizes, and determination of hatching temperatures for the various populations. We must await the final evaluations and their review by other scientists. Should Christopher be correct, it could solve the questions pertinent to how this "species" is able to inhabit such diverse environments.

We have presented habitat data in such a way that should *B. coloradensis* ultimately be divided into three species you will be able to refer the appropriate information to the correct one.

Whatever the outcome, *Branchinecta coloradensis* (or its species complex) is a fairy shrimp that has been known for a long time, but about which we are only beginning to be informed. The range of temperature over which cysts from its various populations hatch is undocumented, but Maynard (1977) observed rather large metanauplii (0.73 mm in length) appearing in water accumulating from melting snow. In her study pools 2,900-3,100 m high in the Uinta Mountains of Utah, growth to maturity took 18-26 days, the longer period being required when melt-down occurred earlier in the season (the temperature relationship holds true again!). Females produced one clutch of 12-33 large cysts (0.39 mm) during a life that spanned the tenure of their pools (45-60 days). Hill and Shepard (1997) measured cysts from 6 California populations. Their data fell into two groups. One averaged only 0.27 mm, but the mean of the other (0.35 mm) was nearly as large as that for cysts from Utah – the same great variability seen for *Streptocephalus sealii*. Still, the overall average of 0.31 mm shows that *B. coloradensis* makes a rather large cyst. Wouldn't it be interesting to know if the populations producing smaller cysts come from lower elevations, and whether their cysts yield nauplii instead of metanauplii?

This species is usually collected between March and July, but Maynard's (1977) statements suggest that her high-elevation Utah shrimps persisted until mid-September. Similarly, individuals seen on October 6 in an icing-over aestival lake in the high Sierra (Pioneer Basin) were probably from a late hatch as indicated by the 3,400-m elevation. This seems a reasonable conclusion given that dates of all collections from our state correlate directly with elevation.

In California, *Branchinecta coloradensis* has appeared in basins from 20 m^2 to 2.6 km long, and all snow-melt ones were annually predictable. Properties of the high-mountain waters have rarely been measured, but what data exist show low pH (5.3-6.8), and very low alkalinity (1-11 ppm) and TDS (10-33 ppm) (Horne 1967; Maynard 1977; Hill pers. comm.). The few records from its Great Basin Desert waters (California and Oregon) show the animals tolerate pH from 7.5-8.5 and alkalinities of 86-290 ppm (Coopey 1946; Lynch unpubl.; Eriksen unpubl.). Even though the water chemistries of Panamint Dry Lake and the alkaline pool on the Sacramento NWR were within these ranges when Clyde sampled them in 1995 (except that the playa was higher in alkalinity, 366-520 ppm), this species was absent. Although most populations of *B. coloradensis* hatch in cold water, all face later-season temperatures as high as 26°C. And like other cold-water anostracans, *B. coloradensis* has been seen in the same California pools with other species of fairy shrimps only a few times (once with *B. mackini*, several times with *Eubranchipus serratus*).

Branchinecta dissimilis

(Map 5.5, p. 121)

This uncommon fairy shrimp seems to have similar requirements and distribution in Oregon and California as does *B. coloradensis*. In the Great Basin, *B. dissimilis* is known only from alkaline pools in Deschutes, Harney, and Lake counties, Oregon (Lynch 1972; Eriksen unpubl.), and Storey County, Nevada (Handelin pers. comm.). In the high Sierra Nevada, somewhat over a dozen of its glacially-formed domains have been located between Monitor Pass south of Lake Tahoe and the high country southwest of Bishop in Inyo and Fresno counties, a total distance of only 150 km. All were at or above timberline from 2,540-3,450 m in elevation. East of Bishop is the only known site for a fresh-water anostracan amongst the non-glaciated topography of the White Mountains. Marilyn Meyers, a graduate student at U.C. Berkeley, netted *B. dissimilis* in a pool 9 km south of White Mountain during the summer of 1995. At 3,587 m, this is the highest recorded anostracan locale in both California and North America.

We commented above that *B. dissimilis* is an uncommon fairy shrimp, but as is often true in ecological matters, such a conclusion may be an artifact of where people have looked. For example, both Karen Wilson and Christopher Rogers went looking for fairy shrimps on the Modoc Plateau in Shasta and Lassen counties, and found populations of this species as low as 1,000 m near Fall River Mills.

Sierra Nevada haunts of *B. dissimilis* are mud-bottomed, yet filled with clear but sometimes tea-colored water, and have measured surface areas of 49-12,800 m^2 (Jim Muck pers. comm.). Because they are in alpine, glacially-scoured granitic basins, these pools and lakes are seasonally astatic or aestival. At the White Mountain site, the 7x5x0.6 m, cobble-bottomed pool contained "very pigmented, reddish-brown" water (translation: high in tannic acids) (Meyers pers. comm.).

Collections were made in March in the Fall River area, and from June to mid-September in the high Sierra and White Mountains. Temperatures were 7.5-23°C. The few data available show that pH of 5.5-6.5 correlates well with low TDS (10-40 ppm), and alkalinity (1 ppm) of the mountain sites. The Great Basin desert habitats of Oregon, though seasonally astatic and filled by snow-melt, differ by being turbid, displaying a pH of 7.5-9.0, and occurring at elevations around 1,500 m (Lynch 1972). Somewhat intermediate conditions were noted by Mark Handelin in a Great Basin Desert pool lying at 1,969 m in Storey County, Nevada, a few km southeast of Reno. Mark sampled several times over the 1995 season, and recorded temperatures from 5.2-20.3°C, low TDS (about 30-160 ppm, from conductivity), and pH of 5.8-7.8.

Because of its distribution, *B. dissimilis* is suspected to produce large cysts which release metanauplii into cold waters yielded by melting snow. However, conjecture is the name of the game for there are no pertinent field observations, and Hill and Shepard (1997) provide the only measurements of cysts. These averaged 0.27 mm, the same as they determined for Sierran *Streptocephalus sealii*, and one of the larger produced by California's fairy shrimps.

Although the range of *Branchinecta dissimilis* in the Sierra Nevada overlaps the southern end of the distribution of *Streptocephalus sealii*, it was the dominant fairy shrimp at elevations exceeding 2,500 m. However, four collections of *B. coloradensis* from above 3,000 m show the latter to be up there as well. *Branchinecta dissimilis* has not been collected with other anostracan species in California, but in a pool in the Great Basin Desert of Oregon it was recorded once with *B. mackini* (Lynch 1972).

Fairy shrimps of cool-water pools which are low to moderate in dissolved solids, moderately predictable, and long-lived

Branchinecta conservatio

(Map 5.6, p. 122)

Branchinecta conservatio was the first organism to be named in honor of The Nature Conservancy, an organization in the forefront of conserving natural diversity, and whose Vina Plains and Jepson Prairie preserves protect two of the few pool clusters which sustain this rare creature, Federally listed as endangered.

This fairy shrimp is found in grasslands of the northern two-thirds of the Central Valley, spanning a north-south distance of about 300 km, at elevations of 5-145 m. Within this limited range, its populations are even more restricted, occupying only a few disjunct localities: the Vina Plains of Tehama County; Sacramento NWR in Glenn County; Jepson Prairie Preserve and surrounding area immediately east of Travis Air Force Base, Solano County; Mapes Ranch west of Modesto, Stanislaus County; near Haystack Mountain northeast of Merced, and the San Luis NWR, in Merced County.

Rumor has it that a highly disjunct population occurs about 340 km to the south near the Ventura County village of Stauffer, at the also anomalous elevation of 1,700 m. This information came from Mike Fugate who raised animals from cysts contained in a dirt sample given to him when he was a graduate student at U.C. Riverside. Clyde attempted to verify this seemingly uncharacteristic location on April 1, 1996; he found a wet meadow, but no pool basin – and that's no joke! Until this population is further documented, we consider its existence anecdotal.

All known pools containing *B. conservatio* are seasonally astatic. In the Vina Plains, basins that hold vernal pools are of the Northern Hardpan type and occur in swales of old braided alluvium derived from the volcanic Tuscan Formation. Jepson Prairie basins are of the Northern Claypan type and form as large playa-like depressions on deep alluvial soils of Pescadero Clay Loam (Keeler-Wolf *et al.* 1995). Origins of the other pools are unknown. All sites are filled by winter and spring rains and usually last into June.

Branchinecta conservatio has been taken from November to late April, when pool temperatures were as low as 5°C early in the ponding cycle, to as high as 24° near the end of the season (Syrdahl 1993). Little other ecological information is available for this species. However, the type locality was studied by Barclay and Knight (1984). They describe Olcott Pond on the Jepson Prairie Preserve as covering about 4 ha with a maximum depth of 30 cm. Clays from its bottom are swept into the water by wind-mixing and the activity of animals, resulting in such turbidity (a white disc disappears at 5 cm) that rooted vegetation is absent except in shallows around its edges. All pools containing this species were at least moderately turbid and most were rather large; the smallest was 30 m^2. Barclay and Knight's data, and Syrdahl's (1993) and ours from the Vina plains, show habitat pH straddling neutral (6.8-7.5), with a few readings of 8.0, and TDS (mainly 20-60 ppm) and alkalinity (16-47 ppm) are both very low.

Brent Helm (1998) provides almost all the information about the biology of *Branchinecta conservatio*. He notes that hatching occurs in the week after pool filling at temperatures around 10°C, and that at least 19 days are required to reach maturity if pool temperatures slowly increase to at least 20°C. However, the average time to maturity, 49 days, demonstrates not only that cooler temperatures slow development, but that this species normally requires a longer time to mature than do others found within its realm. Its cysts (mean diameter of 0.23 mm; Hill & Shepard in press) are comparatively small for California fairy shrimps, and are produced in rather large, though uncounted, numbers. Individuals have lived as long as 154 days in Brent's back-yard rearing pools; however, 123 days was the average longevity. Because only one cohort is produced each year, both sexes normally disappear long before their native pools dry, apparently males first, because they appear to be less tolerant of stressful conditions than females (Serpa, pers. comm.)

Branchinecta conservatio occurs sympatrically with *B. lynchi* and *Linderiella occidentalis* on the Vina Plains (Tehama County), at the Jepson Prairie in Solano County, and near Haystack Mountain and on the San Luis NWR Complex in Merced County. Though it seldom appears in the same pools with these species, one of its rare co-occurrences with the pair also included *B. lindahli*, this at the San Luis NWR Complex. We hasten to remind you that *B. conservatio* not only occurs in great numbers by comparison to these other species, but that it is an especially hyperactive swimmer and filter feeder. You might wish to refer to page 41 to review how these factors are thought to influence the co-occurrence of *B. conservatio* and *B. lynchi*.

Linderiella occidentalis

(Map 5.7, p. 123; front cover)

Ah, *Linderiella occidentalis*, that wonderful red-eyed California endemic fairy shrimp (check out its picture on the front cover) that wiggled in our dip-nets, swam gracefully in the gallon pickle jar that Don Wootton always carried to the field to display our catches, and stimulated Clyde's career-long interest in these graceful creatures! It is the most common inhabitant of cool, soft-water pools of California's Central Valley grasslands. Here, at elevations from 40-168 m, it ranges from near Redding in the north to as far south as Fresno County, mainly to the east of the Sacramento and San Joaquin rivers. In the Sacramento area, it crosses the Valley and enters the Central, then the South Coast, Mountains Regions where it appears in a series of disjunct populations from Willits and Boggs Lake (430 and 850 m in elevation, respectively) in Mendocino and Lake counties north of San Francisco Bay, to Ventura and Santa Barbara counties far to the south. In the last county, where housing for the University of California at Santa Barbara now sprawls, Don Wootton and Clyde collected *L. occidentalis* just back from the sea cliffs, 10 m above the surf; and in the nearby backcountry, on the wildflower-painted slopes of Cachuma Canyon, they dipped this little gem from the highest pool (1,159 m) in which it is known.

Linderiella occidentalis has been netted from late December to early May, at 5-29.5°C (Syrdahl 1993). According to Helm (1998), it is the most tolerant of warm water, and consequent low dissolved oxygen, of all fairy shrimps endemic to the Central Valley. In fact, *L. occidentalis* may thrive in some of these pools until they perish, not from heat stroke, but from desiccation. This species occurs in basins with a variety of geological origins (e.g., Northern Hardpan in old braided alluvium, Northern Volcanic Ash Flow, earth slumps, depressions in lava flows and sandstone caused by weathering) which are filled by winter and spring rains and are seasonally astatic. Most of its residences are vegetated California Vernal Pools (Helm 1998), and contain clear though often tea-colored water. However, not uncommonly, *L. occidentalis* swims in mud-bottomed habitats with lightly turbid water. Although the basins vary in size from a sandstone depression of one m^2 to the 40-ha Boggs Lake, Helm (1998) says that this anostracan typically occupies reasonably large pools; in the Central Valley, only *B. conservatio* frequents larger and deeper habitats. Data on water quality show *L. occidentalis* is a species of poorly buffered soft waters (low alkalinity and TDS, 13-170 and 33-273 ppm, respectively) a consequence of which is that pH varies about a unit to either side of neutral (6.2 to an occasional 8.5).

Cysts of *Linderiella occidentalis* average 0.26 mm in diameter (Hill & Shepard in press). These hatch at most temperatures below 20°C, but the best hatching rate is achieved around 10°C, a common early-season mean temperature throughout its range (Lanway 1974; Helm 1998). Of the Central Valley endemic fairy shrimps, *L. occidentalis* requires the greatest minimum time to reach maturity (31 days), although its 45-day average time to maturity is about four days less than *B. conservatio* which takes the longest. Finally, it holds the record among these species for longevity, 168 days or 6 months, though the mean time of its tenure is 139 days (Helm 1998).

Linderiella occidentalis has been collected infrequently with *Branchinecta conservatio*, but it often co-occurs with *B. lynchi*, in which case *Linderiella* heavily predominates.

Linderiella santarosae

(Map 5.7, p. 123)

This species, restricted to the grassland pools atop the 625-m-high Santa Rosa Plateau in Riverside County, has only recently been described (Thiéry & Fugate 1994). Eng, Belk, and Eriksen (1990) thought these fairy shrimps were *Linderiella occidentalis*, isolated by some 300 km from their nearest populations in Ventura and Santa Barbara counties. Accordingly, habitat information for Santa Rosa Plateau pools were lumped with all the rest of the field data for that species. Once the few facts pertinent to the Santa Rosa Plateau were separated, and data for both species compared, their habitats appear similar – as perhaps one should expect. That they are sometimes shared with *Branchinecta lynchi* should perhaps be expected as well.

Linderiella santarosae resides in Southern Basalt Flow Vernal Pools (Keeler-Wolf *et al.* 1995; Zedler 1987) ranging from 25 to just over 100,000 m^2 in area. These basins are filled by winter and spring rains, and the water is usually clear to lightly milky, although one disturbed pool contained red-turbid water. Recorded temperatures span 9.5-21°C, while pH is 6.3-8.5 and TDS (from conductivity) is low (90-195 ppm; Collie & Lathrop 1976; Keeley 1984; Eriksen unpubl.).

Nothing is known about the biology of this species except that its cysts are moderate in size (average 0.28 mm; Hill & Shepard in press). Until further information is accumulated, we should probably assume its life requirements are similar to those of *L. occidentalis*. Even though the range of *L. santarosae* is small and its pools are but a handful, The Nature Conservancy's Santa Rosa Plateau Preserve protects this most restricted of California's endemic fairy shrimps.

Fairy shrimps of cool-water pools which are low to moderate in dissolved solids, less predictable, and short-lived

Branchinecta sp.

(Map 5.8, p. 124)

This new species of *Branchinecta* is presently being formally described. Because it has been found only in the center of the Central Valley (at elevations around 20-90 m in Fresno, Madera, Merced, Sacramento, San Joaquin, and Solano counties), it is referred to as the "midvalley fairy shrimp", a name we will use in absence of the publication of its formal scientific handle.

Except for cyst measurements (diameter of 0.27 mm; Hill & Shepard in press), Brent Helm (1998) has provided all our information on the natural history of the midvalley fairy shrimp. Like other Central Valley grassland endemics, cysts hatch in the first week of pool filling if water is in the neighborhood of 10°C. When conditions are optimal, that is when temperatures slowly increase to at least 20°C, maturity is reached in 16 days, the shortest time for any of the California fairy shrimps. However, its average of 45 days to maturity, indicates that *B. lynchi* (typically 41 days) and *B. longiantenna* (mean of 43 days) normally attain this stage more quickly. As to its maximum time on earth, some midvalley fairy shrimps have hung in there for 143 days, or just a little over 5 months, although the mean was 123 days. Amongst California endemics, only *B. lynchi* displays a lesser maximum longevity. However, the midvalley fairy shrimp could seldom live so long because it typically occurs in small, unpredictable, grass-bottomed vernal pools and puddles in the most ephemeral of seasonal wetlands (Helm 1998). In such transitory real estate, a new cohort will hatch each time the basin refills with water of approximately 10°C. This species has been collected from late January to early April, and only three times has it been taken with another anostracan (*B. lynchi*).

Branchinecta longiantenna

(Map 5.5, p. 121; front cover)

Now here is an interesting-looking creature (check out its mug shot on the front cover; also see Fig. 7.19, p.158). Because its antennae are far longer than any other North American species, it is referred to as the longhorn fairy shrimp.

Branchinecta longiantenna also has an interesting and restricted distribution. The few known sites lie near the eastern edge of the Central Coast Mountains Region, and it is one of four California endemics Federally listed as endangered. Beginning at the northern end of its range, in the foothill grasslands west of Tracy, it has been dipped from 8 clear-water depression pools in sandstone outcrops. The first of these hauls was made in 1937, long before this beast was even scientifically described. In 1981-1982 Larry Eng and his associates made all but one of the remaining collections. All these localities are within 10 km of each other, spanning the border of Contra Costa and Alameda counties.

Located about 100 km to the southeast, in the Central Valley but only 25-30 km from the eastern foothills of the Central Coast Mountains Region, in Merced County, is the Kesterson NWR. Here, at an elevation of 23 m, Michael Peters first found *B. longiantenna* in 1993 swimming in 8 of 70 or so clustered grassland pools. However, in a beautiful demonstration of environmental capriciousness, during the dryer winter and spring of 1994 it appeared in only one.

Another jaunt, 235 km to the south-southeast, brings us to the southern most sites harboring our longhorn friend. Around the borders of Soda Lake in San Luis Obispo County are many vernal pools of the Northern Claypan type (Keeler-Wolf *et al.* 1995). From 1983-1988, Bob Brown, then Bob and Clyde, found at least 13 basins which serve as home for *B. longiantenna*. It also lives in a number of pools on The Nature Conservancy's Preserve in the Soda Lake area (Larry Serpa pers. comm.). These sites are in lightly alkaline soils and are scattered amongst grassland and Valley Saltbush Scrub (Keeler-Wolf *et al.* 1995), near the eastern edge of the Central Coast Mountains Region, at elevations around 590 m.

Branchinecta longiantenna has appeared from late December to mid-May in basins filled by winter and spring rains. In its tiny clear-water depression pools in sandstone, temperatures from

10-18°C have been recorded but no water chemistry was undertaken. However, given some work that Clyde did in a rock pool elsewhere, and the fact that sandstone is very low in soluble substances, we can reasonably assume that pH is in the neighborhood of 6.5-7.0, and TDS and alkalinity are very low. By contrast, *B. longiantenna*'s clear to rather turbid, clay- and grass-bottomed pools, 1-62 m in diameter, exhibited temperatures from 10.0-28.0°C. No observations have been made on predictability or longevity of these waters, however, given their positions in the rain-shadow of the Central Coast Ranges, they are undoubtedly less predictable, and probably short-lived (Bob Brown estimates about three weeks). TDS (130-590 ppm) and alkalinity (58-156 ppm) are low to moderate, as they are in habitats of other grassland fairy shrimps, but the range of values is slightly greater. A median pH of 7.2, with a range of 6.7-7.9, is similar to that of other grassland species as well.

Branchinecta longiantenna certainly vies for the distinction of being one of the least known of California's fairy shrimps. Several of Clyde's students studied it, two of its tolerance of heavy metals (Mizutani *et al.* 1991), another its filter-feeding rate (Patten 1980). Mizutani (1982) also used this species to develop a model demonstrating how a clay particle, dissolved organic molecules, and bacteria form a complex large enough to be filter fed by anostracans (see p. 50 in section: What do fairy shrimps eat?).

Once more Brent Helm (1998) provides our only information on natural history. Like other Central Valley endemics, larvae of *Branchinecta longiantenna* hatch soon after winter and spring rains fill their swimming pools with water hovering around 10°C. We assume they emerge as nauplii because the average cyst diameter of 0.26 mm (Hill & Shepard in press) falls within the size range of others which do so. In any event, whatever pops forth, these shrimps need temperatures of 15-20°C to attain maturity. If conditions are optimal, maturation is reached in 23 days, more typically it requires 43 days. If their pools remain for an extended period of time, then individuals of *B. longiantenna* are known to swim right along for up to 147 days.

The preceding is interesting and ultimately useful information, but none of it helps much to explain why the distribution of this species, and its co-occurrence with other anostracans, is so restricted. We do not know why it is tucked away only in or near the eastern foothills of the Central Coast Mountains, nor do we clearly understand why it and *Branchinecta lynchi*, which also lives in the three major areas where *B. longiantenna* occurs, have only twice been found together. For example, in its small rock pools, with but one exception, *B. longiantenna* apparently swims alone, although these are very close to other seemingly identical sites that contain only *B. lynchi* or *Linderiella occidentalis*. *Branchinecta conservatio* and *B. lindahli*, as well as *B. longiantenna* and *B. lynchi*, share the Kesterson pool complex, but each claims its separate residences. In the Soda Lake area, only once were *B. lynchi* and *B. longiantenna* taken together. The latter has been found a few times with *B. lindahli* around Soda Lake, but co-occurrence has not been observed at Kesterson. Ah, as yet there still remain some very private lives amongst fairy shrimps!

Branchinecta lynchi

(Map 5.9, p. 125; Fig. 1.2, p. 2)

Branchinecta lynchi is an uncommon, common fairy shrimp. How's that for a seeming contradiction? Consider the beast common because it appears to be rather widely distributed in the grasslands of the state, from near Red Bluff in Shasta County, south through much of the Central Valley, and ultimately via several disjunct populations to the Santa Rosa Plateau in Riverside

County in the South Coast Mountains Region. Deem it uncommon because *B. lynchi* is not abundant anywhere; and when it co-occurs with other fairy shrimp species, which is reasonably often, it is always far outnumbered.

Throughout its range *Branchinecta lynchi* has been taken from early December to early May. In and near the Central Valley, its residences range from about 10-290 m in elevation; in the South Coast Mountains Region some are as high as 1,159 m. Habitats are of two major kinds. One, which includes the type locality, is restricted to the Slanted Rocks area west of Byron Hot Springs in the southeast corner of Contra Costa County. There, clear water is held in small depressions, usually less than 1.0 m diameter, in sandstone outcrops which are surrounded by foothill grasslands. These puddles each contain only a few shrimps which face unknown water quality, though alkalinity and TDS are undoubtedly quite low. The more common habitat is a small swale, earth slump, or basalt-flow depression basin with a grassy or, occasionally, muddy bottom, in unplowed grassland. Normally these are smaller pools than those occupied by other Central Valley anostracans (except the mid-valley fairy shrimp). These are predominantly the California Vernal Pools discussed by Holland (1978), Keeler-Wolf *et al.* (1995), Thorne (1984), and Zedler (1987). However, their pool basins display the greatest diversity of origins found amongst Central Valley fairy shrimp haunts, and this variety includes disturbed and constructed sites unfavorably received by other species (Helm 1998). These places of residence vary dramatically in size, from one exceeding 10 ha, to an uncommonly small puddle only 3 cm deep and covering but 0.56 m^2. *B. lynchi* occurs in waters at least 4.5-23°C, with low to moderate TDS (48-481 ppm, mean of 185) and alkalinity (22-274 ppm, average of 91), and a mean pH of 6.8 with a range of 6.3-8.5 (Collie & Lathrop 1976; Keeley 1984; Syrdahl 1993; Eriksen unpubl.).

Branchinecta lynchi can beget cysts speedily, which places it in the company of the midvalley fairy shrimp and *B. lindahli*, both of which have similar hurry-up-and-reproduce adaptations. For example, Gallagher (1996) and Helm (1998) observed that *B. lynchi*, which hatches soon after water of 10°C or less fills its pools, will reach maturity in close to 18 days under optimal conditions, that is when daytime water temperatures rise to at least 20°C. However, 41 days are more typical if the water remains in the vicinity of 15°C. Helm's records also divulge that, of the Central Valley endemic anostracans, *B. lynchi* has the shortest maximum longevity at 139 days, although 90 was the mean longevity in his artificial backyard pools. Sean Gallagher (1996) studied a cluster of natural pools in Butte County and watched most individuals disappear around 70 days, and vanish completely after about 84 days, even when water remained in their basins.

The number of cysts produced per clutch, and how many clutches can be generated during a life span, are unknown quantities. However, once cysts have been dropped, all that is necessary for another hatching is a frost or major storm which lowers water temperature to around 10°C (Helm 1998). Gallagher (1996) reports three separate hatches in a season, while Helm has observed 6! This ability of being ready and able to launch more than one cohort per year sets *B. lynchi* and the mid-valley fairy shrimp apart from other Central Valley endemic anostracans.

These biological realities certainly paint a telling picture of why *Branchinecta lynchi* dwells in some of the shortest-lived of fairy shrimp settings – pools which persist for only 6-7 weeks in winter, and perhaps three weeks in spring. Since *B. lynchi* develops faster in warmer spring pools than in colder winter ones, it probably averages about a week of cyst production unless individuals dwell in deeper longer-lived pools. In the latter situations they commonly co-occur with *Linderiella occidentalis* and, on the Santa Rosa Plateau in Riverside County, with *L. santarosae*.

The wide general distribution of *Branchinecta lynchi* overlaps or interfaces with the ranges of a number of other anostracans. Even so, we are aware of *B. lynchi* rubbing phyllopods only once or a couple of times with *B. mackini, B. lindahli, B. longiantenna*, the midvalley fairy shrimp , and *B. conservatio*. Brent Helm believes he knows why *B. lynchi* can't tolerate the last. To refresh your memory of the intimate details, refer to page 41 in the section on "Coexistence".

Branchinecta lindahli

(Map 5.10, p. 126; Fig. 5.3, p. 116)

If you thought *Branchinecta lynchi* had a knack for getting around the state, then consider *B. lindahli*. In the Great Basin Desert of California this vagabond has staked a claim to some turf near Ravendale in eastern Lassen County at around 1,600 m elevation. Further south it has set up shop mainly in the western two-thirds of the Mojave Desert (500-1,200 m elevation) and across the Tehachapi Mountains it is established in the arid portions of the western half of the Central Valley less than 90 m in elevation. The species is also found west of the Central Valley in disjunct, low elevation, arid areas where pools are short-lived; known sites in the Central Coast Mountains Region are near San Jose in Santa Clara County, at Fremont and Livermore in Alameda County, and around Soda Lake in San Luis Obispo County. In the South Coast Mountains Region, our amazingly versatile fairy shrimp dwells in all coastal counties from Ventura to San Diego. Of course, everyone "knows" fairy shrimps were wiped from the L.A. Basin long ago, but, guess what, Mark Angelus just reported a fugitive population of *B. lindahli* hanging tough at the Madrona Marsh Nature Preserve in Torrance. Knowing it had been reported from Santa Cruz Island off the southern California coast, Chad Soiseth (1994) set sail to Santa Rosa, San Miguel, and San Nicolas Islands where he found populations as well. *Branchinecta lindahli* is also widespread outside of California, being known from Baja California, Mexico, including Guadalupe Island, and from all states west of the Rocky Mountains except Idaho, and on the Great Plains from southern Alberta to Kansas.

Our subject has been seen "doing its thing" from late November to early June in seasonally astatic pools and puddles which collect water from winter and spring rains. These habitats are typically unpredictable, often quite small, and short-lived. They vary considerably in type and origin, from playas, to arid grassland swale pools, small water-filled gas pockets in old lava flows, and depressions created by weathering of sandstone and quartz monzonite domes. Some of the sites, although natural to begin with, have been highly disturbed and modified by a menagerie of ORVs, and by junk heedlessly dispensed by a coterie of users. Excavated depressions, where sub-surface soils are exposed to water that overlies them, are seldom suitable habitats for fairy shrimps. However, in arid environments where surface clays readily erode and are carried by wind and water into road-side ditches, quarries, bulldozed watering holes, even tire ruts, these human-constructed habitats may suffice for the seemingly ever-tolerant *Branchinecta lindahli* (another of Clyde's and Denton's observations).

Given its preference for arid lands, you should not be surprised that their milieu is typically turbid, yet *B. lindahli* also swims successfully through clear-water pools. Individuals of this species are equally flexible with water chemistry. Not only do they appear in very soft waters, as low in TDS and alkalinity as for any California anostracan, but they also frolic, though much less frequently, in pools that have measured as much as

3,000 ppm TDS in California, and even 23,000-37,440 ppm (from conductivity and specific gravity) in Wyoming and Nebraska (Horne 1967; Lynch 1964; McCarraher 1970). Alkalinities up to 763 ppm (one at 2,406 ppm) have been recorded for California, while McCarraher (1970) lists the astonishing value of 10,030 ppm for By-Way-Ranch Pond which lies amid those strange sand hills of Nebraska. These are ionic levels tolerated routinely only by *Artemia franciscana* and *A. monica*, and occasionally by *Branchinecta mackini* and *B. gigas*.

Gonzalez *et al.* (1996) have explained *Branchinecta lindahli*'s apparent indifference to habitat by its ability to regulate hemolymph concentration (at least of Na^+) considerably above that of the environment in water of very low TDS (up to 460-690 ppm of Na^+), while, in contrast to obligate soft-water species, above that amount it tolerates increasing concentration of Na^+ in its blood to at least 2,300 ppm (from mmol/L) (pp. 19-20 in section on: Water, salts, and liquid wastes...).

While the range of pH measured in its habitat (6.7-9.8) was greater than for any other fairy shrimp in California, *B. lindahli* is not so versatile with temperature. Thermal conditions in which it has been recorded (1.5-22.2°C) must certainly be considered moderate. Habitat records from outside California demonstrate a wider tolerance, however. For example, in Wyoming, Horne (1967) found *B. lindahli* at temperatures from 1-32°C, and Denton, who as a Texan is not prone to heat stroke, collected some in an Arizona pool with a temperature of 34.5°C (Belk 1977a). And, with regard to pH, back in those enigmatic Nebraska sand hills McCarraher (1970) netted *B. lindahli* in a "strongly alkaline pond with water the color of black ink", and at a pH of 10.0. Perhaps we have here California's fairy-shrimp equivalent of the "renaissance man".

Many of the habitat preferences of *Branchinecta lindahli* can be explained, of course, by others of its biological abilities. For example, hatching happens best from 5-20°, poorly at 25°, and not at all at 30°C (Belk 1977a). This means that although nauplii can emerge readily in cold temperatures, cysts also hatch in cool water typical of spring in arid portions of California. At the other end of its temperature spectrum, Denton recorded a one-hour LD/50 (remember, this is not an ecological measure, only a lab comparator) of 36°C, this being intermediate among the coldest- and warmest-water Arizona species with which he worked. Thus, the temperature physiology of *B. lindahli* explains, at least in part, its occurrence from mid-December to mid-May in the milder portions of California. An inability to hatch in warm water accounts for its absence in summer.

The wide range of ionic concentrations in which nauplii of *B. lindahli* appear (up to 3,000 ppm; Horne 1967) is certainly another of the reasons for why this species occurs over such a broad array of TDS. It also demonstrates that the mechanism for suppressing hatching is unlike the one for *B. mackini*, a species with which it may coexist, and for which hatching is arrested at TDS levels greater than 1,000 ppm (Brown & Carpelan 1971).

Hatching of *Branchinecta lindahli* cysts yields nauplii averaging 0.25 mm in length, and, not unexpectedly, the rate of their further development is controlled by temperature. In inland North America, at low elevations along the Rocky Mountain front, 17-20 days are required to attain maturity in the cold and cool of spring (April-May), but only 9-13 days in the warmth of summer (June-September) and fall (October-November) (Maynard 1977; Donald 1983). On bluffs overlooking the Pacific Ocean near Oceanside, San Diego County, on January 16, John Moeur (pers. comm.) found rather large fairy shrimps swimming at 11°C in rain water which had filled an "industrial-sized tire rut" between January 2 and 3. What daytime temperatures these denizens of the rut had basked in for two weeks is not known, but remember that winter here is not a bone-chilling experience. During those 13-14 days, not only had *B. lindahli* made its appearance, but so had *B. sandiegonensis*; and both had passed through adolescence and already had the opposite sex in mind.

Maynard (1977) noted that most pools in which *B. lindahli* lived lasted only 5-30 days, with the shrimps succumbing only when pools dried; however, she did indicate that some individuals survived up to 106 days when water remained that long. Maynard's work also indicates that *B. lindahli* invests much energy in early development and maturity but does so at the expense of the sizes of its body, clutches, and cysts. For example, in a summer puddle lasting only 10 days, individuals reached maturity at an average length of 6.7 mm, a size that severely limited the number of cysts produced per clutch (minimum of 3) even though the cysts were of moderate size (0.28 mm average; Arizona cysts 0.26 mm, Belk 1977b; those from California 0.24-0.27 mm, Hill and Shepard 1997, and Moeur pers. comm.). As a consequence, the average fecundity was only 16. Spring pools generally lasted longer, and as their duration increased so did the sizes of females and their clutches, and the number of clutches, so fecundity was greater. Maynard drew her conclusions from the following data: while females 8-12 mm long generated around 25-50 cysts per clutch, females 20 mm long (the largest in her study) averaged 150. As a consequence, in a pool which lasted 14 days, female fecundity averaged 192 cysts; in a 33-day pool, 213 cysts; and at a 77-day site, females yielded a mean of 326 cysts.

For the sake of perspective and ecological comparison, remember that *B. lindahli* is often found in habitats similar to those of *B. mackini* but shorter-lived. Maynard's data show us that *B. mackini* takes so long to develop it can not reproduce in the more temporary habitats, like the 14-day site just noted. However, when pools containing these two species persist around 30 days or longer, females of *B. lindahli* muster only one-third as many cysts as their competitor. Maynard argued that these biological differences work to the disadvantage of *B. lindahli* in longer-lived waters, while such a strategy offers them the upper hand in smaller and more temporary habitats, and in drought years. Also, the possibility that drought one year enhances hatching the following year (Donald 1983) provides an explanation for the occurrence of *B. lindahli* in some of California's smallest, most temporary, and unpredictable puddles and pools.

Not only is *Branchinecta lindahli* especially tolerant of a wide array of physical and chemical conditions, it shows the greatest flexibility in acceptance of other species of fairy shrimps. Check out Table 3.1 (p. 45) where we name names.

Branchinecta sandiegonensis

(Map 5.8, p. 124)

When Eng *et al.* (1990) wrote their paper on California Anostraca, *Branchinecta sandiegonensis* had not yet been described. At the time it was thought to be *B. lindahli*. But with Mike Fugate's (1993) description of the species, and his and Denton's review of all southern California collections originally thought to be *B. lindahli*, we now know that our San Diego critter is the most frequently found fairy shrimp in a 50 km-wide coastal strip of San Diego County where pool elevations most commonly range from 15-125 m but do reach 500 m. Yes, *B. lindahli* occurs in this strip as well, but, no, it is not common! And, yes, *B. sandiegonensis* has been reported elsewhere. For example, it is known from two pools lying on coastal mesas of Baja California, Mexico, within 70 km of the international border (Fugate 1993; Brown *et al.* 1993), and recently it has been found living with *Streptocephalus woottoni* in a disgusting stock pond in what remains of ranching country that borders suburbia in southern Orange County. In addition, it lives in shallow pools on a mesa perched above the Santa Ana River, also not far from the ocean, and also in Orange County. Although *B. sandiegonensis* has not been reported from Los Angeles or Ventura Counties, there is one report of it (one female only) at Isla Vista, adjacent to the U.C. Santa Barbara campus (Fugate 1993). Because the latter account has not been redocumented, no one knows whether it represents a remnant population in a California distribution that once extended from Santa Barbara to the border with Mexico, or is the result of an inadvertent confusion of samples. Why *B. sandiegonensis* has not made it to the off-shore islands of California and Baja California, a feat which *B. lindahli* performed, is one of those fascinating questions which we hope will tickle the fancy and tantalize the talents of some future watcher of fairy shrimps. If so, perhaps one more unsolved mystery about these worthy creatures can be deciphered. And if it is, perhaps the answer will throw some light on why the distribution of this species is so restricted.

Even though we describe *B. sandiegonensis* as "the most frequently found fairy shrimp within its limited range", do understand that this is a relative phrase, for the animal is under such threat of development, that in February of 1997 the San Diego fairy shrimp was placed on the Federal Endangered Species List (Federal Register 1997).

Branchinecta sandiegonensis may appear when late fall, winter, and spring rains fill their small, shallow (usually less than 30 cm deep), unpredictable, and seasonally astatic puddles and pools (Balco & Ebert 1984). Although there is no consensus on how the basins in which this species swims were formed, there is agreement that they have been with us "...probably at least since late glacial times – 25,000 years or more.", and that they occur on coastal terraces which emerged from the sea as its level fell and the land rose between 100,000 and one million years ago (Zedler 1987). Keeler-Wolf *et al.* (1995) describe both San Diego Mesa Hardpan and Claypan basins as typical of those on the coastal mesas of San Diego County. The former are identified by reddish-colored soils with a cemented iron-silica layer that prevents the percolation of water; they are most numerous on the mesas north of the city of San Diego. These soils are commonly associated with chamise Chaparral, although Coastal Sage Scrub and annual grasslands are occasionally present. The claypan pools are formed in quite fine gray soils which largely support annual grasses. These are concentrated on the Otay Mesa, which lies along the Mexican border, east of the city of San Diego.

In laboratory cultures, females produced 164-479 cysts over their life time (Simovich & Hathaway 1997). These cysts are relatively large (0.27 mm, Fugate 1993; 0.30 mm, Hill & Shepard in press), strikingly larger than those of their closest relative *B. lindahli*. Hathaway and Simovich (1996) note, from lab and field findings, that larvae appear in cool water of 5-15°C, but not at temperatures between 15-20°C. Moeur says "they write as if it's a simple task to hatch cysts of *B. sandiegonensis*...but it isn't! I had one helluva time getting a few nauplii to pop out, and I don't know what signaled those few to make their appearance". In actuality it wasn't such a simple task for these researchers either as is indicated by one of their later papers (Simovich & Hathaway 1997). In it, they specify that just 6% of cysts hatch at first wetting (range of 0-33%), and by the end of three hydrations a total of only 28% had released nauplii. They go on to say, however, that these numbers underestimate hatching success, for, in an analysis of a separate batch of cysts, only 50% contained embryos. Whichever low number you prefer, there is a bright side to having so few emerge at each wetting. Because the pools in which *B. sandiegonensis* resides are small and shallow, and because heavy rainfall in southern California is anything but predictable, the water that accumulates may vanish before the animals reach maturity. Under such circumstances, not having a high percentage of your cysts hatch with the first alluring presence of water makes a lot of ecological sense.

The few data we have on the subject show that nauplii emerge and develop to adults sometime between mid-December and early May. At these times water temperatures vary between 10-26°C (Simovich and Fugate 1992), though John Moeur told us of a sauna-like 31°C reading. pH is moderate (6.5-8), and alkalinity (40-55 ppm) and TDS (mean of 75 ppm, as measured by conductivity) are low (Balco & Ebert 1984; Gonzalez *et al.* 1996; Moeur pers. comm.). The reason for these chemical preferences seems to be that individuals of *B. sandiegonensis* strongly hyperregulate the ion concentration of their hemolymph in waters of low TDS. However, when concentrations in the habitat rise above normal body levels, the animals are no longer able to regulate, their hemolymph Na^+ elevates, and they die (Gonzalez *et al.* 1996).

Only Hathaway and Simovich (1996) have delved into the reproductive and developmental biology of *Branchinecta sandiegonensis*. They note that cysts require 8 days to hatch at 5°C, but that period is shortened to 3-5 days at temperatures between 10-15°C. Higher temperatures do not result in a hatch. Once larvae appear, they will ultimately die if maintained at 5°C, but if the lab temperature is raised and kept at 20-22°C, they mature in 7-10 days. In the field where temperatures oscillate, 10-20 days must pass before animals become mature. Once that happens our little bundles of joy live on for as much as another three weeks (maximum longevity being 42 days). Such biological limits fit this species well to its small, unpredictable pools in coastal, sunny southern California.

Branchinecta sandiegonensis, unlike its "cousin" *B. lindahli*, usually swims in the absence of other anostracans. And even though *B. lindahli* and *Streptocephalus woottoni* are the only fairy shrimps that occur within its range, another of those intriguing questions is why, when *B. lindahli* is so ubiquitous and apparently tolerant of other species, has it been collected only a couple of times with *B. sandiegonensis*? Competition seems the most likely reason, but no one really knows. *Branchinecta sandiegonensis* has been noted a bit more frequently with *S. woottoni*, but even this seems odd, because while the former is more typically a resident of shallow, shorter-lived habitats, *S. woottoni* lives in deeper, longer-lived pools.

Fairy shrimps of cold- and cool-water pools which are moderate to great in dissolved solids, predictable to less predictable, and long-lived

Branchinecta mackini

(Map 5.11, p. 127)

Branchinecta mackini is not at all like the red-eyed fairy shrimps that swam in grass-lined pools of clear water with which Professor Donald Wootton entrapped Clyde's life-long fascination with anostracans. To the contrary, the eyes of these guys are black, and the shrimps see next to nothing as they ply alkaline waters made brown with clay stirred up from the soft mud bottoms of their pools and playas. Colorful? An inhabitant of pastoral settings? It depends on how you view muddy water that lacks aquatic vegetation; but *Branchinecta mackini* is a cherished favorite none the less, for this is the fairy shrimp with which I, Clyde, entrapped my own students, the first of which was Robert J. Brown. It all began in 1962 on a field trip I was leading. We were dipping nets into a sag-pond along the San Andreas earthquake fault (to the chagrin of several class members) when up came a haul of wriggling fairy shrimps. I got excited, Bob seemed fascinated, and in response to my invitation he relinquished his semester break and we began the studies that took us on many a storied trip to alkaline basins in the Mojave and Great Basin deserts, consumed untold hours on experiments in the lab, and spanned 18 years. Among the end results of these efforts were a PhD for Bob, several co-authored scientific papers, a friendship that finds time even today...for fairy shrimps, and a story involving *B. mackini* that shows you the world is really a small place.

Allow us to digress a bit to spin this story. In the spring of 1964, Clyde was in the backcountry of Santa Barbara collecting fairy shrimps. Wanting access to a pool on private land, I struck up a conversation with the cowboy who managed the area. His eyes lit up as did his hand-rolled cigarette when he stated that fairy shrimps were familiar to him. He told me he was in the desert some years back when a news reporter, and a biologist from CSU Los Angeles, showed up to record creatures swimming in the muddy water of Bicycle Dry Lake. Given the time frame, this was apparently the "adventure" that led to the article in the L.A. Times describing trilobites in the desert (see p. 34 in "The fairy shrimp's aquatic community"), and also yielded a collection that fell to the hands of Ralph Dexter, the scientist who, in 1956, mentioned this locality along with other known harborages when he described *Branchinecta mackini* as a new species.

Bicycle Dry Lake is an alkaline playa, and *Branchinecta mackini* is a fan of alkaline pools wherever they last long enough that the animal's life can undergo its complete cycle. For example, the Great Basin Desert, which incorporates parts of Modoc and Lassen counties in the far northeast corner of California and a relatively small piece of turf from Mono Lake to immediately east of Mammoth Mountain in Mono County, has a number of waters which contain *B. mackini*. These areas lie at elevations from 1,200-2,100 m where most of the pools are probably predictable and seasonally astatic, although a few are perennially astatic and aestival like the 20-km-long Middle Alkali Lake. Basins of internal drainage, also high in alkali chemicals, exist throughout the northwestern three-quarters of the Mojave Desert between elevations approximating 400-1,200 m. And here too *B. mackini* paddles its canoe, but this time in unpredictable pool and ditch habitats, typically associated with playas, where water is present long enough for the animals to mature. *Branchinecta mackini* also spans the Tehachapi Mountains, finding harborage at elevations from 17-99 m in the Great Central Valley, particularly its arid southern third. However, one can find scattered populations in seasonally astatic alkaline waters along the Valley's western edge as far north as Glenn County.

And how alkaline are the waters in which these little beauties swim? And what about the other physical and chemical aspects of their habitat broth? Eng *et al.* (1990) list a mean pH of 8.7 (range 7.0-9.8) which dramatically demonstrates the alkaline nature of its habitat and should prove to you that the alkaline fairy shrimp is pretty well named. In fact, *B. mackini* dwells, on average, in higher alkalinities (maximum of 2,810 ppm, mean of about 1,600 ppm) than any other North American anostracan except *Artemia monica*, which is restricted to Mono Lake. (To find out how much of an exception it is, you will have to read its biography beginning on page 115). *B. mackini* has appeared in alkalinities as low as 146 ppm, but such a low value is rare and may have been the result of runoff temporarily diluting the basin's chemical mix. Known TDS of this creature's pools varies from 486-4,800 ppm (mean of 1,364).

You've got to take your hat off to *B. mackini* and its ability to deal physiologically with the magnitude of these environmental challenges. How does it do it? Opinions vary. Robert Brown (1972) says the animal handles low levels of TDS by regulating its hemolymph hyperosmotically. Broch (1988) agrees, but says the animal doesn't do a very good job of it. He also believes that once the iso-osmotic or isoionic points are reached, *B. mackini* then conforms to increasing environmental concentrations until it dies. Gonzalez *et al.* (1996) appear to corroborate Broch's conclusions although they measured only Na^+, the most common ionic component in this animal's milieu. By contrast, Brown (1972) says that *B. mackini*, both adults and nauplii, can deal with elevated environmental dissolved solids by regulating hyposmotically. Although we may be comparing apples and oranges here, or dealing with different levels of precision because of the methods involved, resolution of what seem to be different scientific findings awaits yet another inquisitive mind.

Because *Branchinecta mackini* is obviously a species of deserts, or areas with desert affinities, it goes without saying (although we're going to say it) that the species does not occur in any of the mountain regions of the state. However, the lowest, hottest desert in California, the Colorado, does not know *B. mackini* either. Consider these possibilities as to why: habitats of sufficient alkalinity are rare to non-existent there; but, should they occur, individuals probably cannot tolerate the extended periods of high temperature which come with the territory; and finally, winter and spring rainfall is probably too slight to provide pools which last long enough for these creatures to reach maturity.

In the Great Basin Desert portions of California, nauplii of *Branchinecta mackini* emerge in the snow- and ice-melt waters of spring where they mature, and remain until their pools disappear through evaporation, or the shrimps reach maximum life expectancy (as long as 107 days; White & Hartland-Rowe 1969). Although the Mojave Desert can get downright cold at night, cold enough to form ice cover on pools, the water in these basins comes not from melting snow and ice but from rain. And when those blessed raindrops fall and coalesce into the runoff of flash-floods, low-lying basins are rapidly filled with water of limited TDS (less than 1,000 ppm), the signal for cysts of this animal to hatch (Brown & Carpelan 1971). These flood and hatching events typically occur in the cold of winter or cool of spring, but on rare occasions a summer storm may lead to a hatch in a tepid pool. Individuals of *B. mackini* that dwell here during summer would not normally achieve maximum possible life expectancy, for water temperatures can become lethal (39°C has been recorded by Brown & Carpelan 1971), or the bath will all too soon climb the evaporative ladder to the bright sunny sky.

Given that *Branchinecta mackini* ranges from southern Alberta and Saskatchewan, south into Nebraska and Wyoming, and westward into most intermontain basins containing alkaline soils from the Rocky Mountains to California's Central Valley, no one should be surprised to learn that its temperature physiology demonstrates the lability just indicated. Although more typically hatching in near-freezing water, and developing to sexual maturity in 21-31 days under cold spring conditions (Maynard 1977), *B. mackini* is sufficiently flexible to produce populations in the warm water of fall and much warmer water of summer. For example, although not mentioning temperatures preceding hatch, Maynard (1977) wrote that only 12-17 days were required for *B. mackini* to reach sexual maturity in her fall study pools near Salt Lake City, Utah. Brown and Carpelan (1971) said nothing about hatching temperatures either, but did indicate that water in a summer puddle formed in Rabbit Dry Lake, a Mojave Desert playa, varied from 12°-32°C during the tenure of *B. mackini*. Although these extremes are experienced only fleetingly in any 24-hour period, that living during a season when water temperatures approach 32°C may be hazardous to this fairy shrimp's health (and survival) is suggested by the observations of Eriksen and Brown (1980b). We placed a small aquarium of water at 22°C containing cold-season animals in a controlled-temperature room set at 34.5°C and let the combo warm. No shrimps survived 10 hours. Five weeks later we followed the same recipe with cool-season forms from the same pool. This time quite a few hung in there for 11 hours, demonstrating that the physiology of *B. mackini* adjusts (acclimates), in this case its upper lethal temperature is raised, as the pool warms through the season.

No matter the time of year, *Branchinecta mackini* matures at about 10 mm in length (Maynard 1972), grows to lengths of 30-32 mm, and produces cysts which average 0.31 mm in diameter (Maynard 1977). Of California's anostracan species, those with such large cysts are basically forms which dwell in predictable snow-melt pools, and hatch as metanauplii. Although *B. mackini* does reside in predictable snow-melt pools, unpredictable rain-formed habitats are more typical, and Maynard says that it pops out of the cyst as a nauplius, albeit a large one (0.56 mm). She also says that variability of cyst size, even in the same clutch, is considerable, citing measurements of 0.22-0.38 mm. Such variability undoubtedly also accounts for the significant size difference recorded by Hill and Shepard (1997) for cysts from California *B. mackini* (0.14-0.32 mm, mean of 0.26 mm). Because the latter diameters are more typical for cysts which release nauplii, we would like to know the length of larvae hatching from them. We think, too, that the person(s) whose curiosity gets titillated by Denton's hypothesis concerning pool temperatures at time of hatch, cyst size, and larval length and developmental state at hatch (see pp. 75-76), would find *B. mackini* a fine experimental animal. This because, like *Streptocephalus sealii* whose physiological and ecological variability stimulated Denton's hypothesis, *B. mackini*'s habitat and physiology span a similar range of conditions. Whatever the outcome of such work, this animal demonstrates the truism that variability is often, if not usually, great! And separating what is genetically caused from what is environmentally influenced is the difficult, but fascinating task for whoever will grapple with the challenge.

With regards to hatching, just what are the conditions that initiate the process? As described above, larvae will appear in water near 0°C, as well as in desert pools during summer; however, no one has worked out exactly what higher temperatures shut down the process or to what degree temperature is involved. According to Brown and Carpelan (1971), the major controller of hatching for this species is not temperature, but osmotic shock from low-TDS water supplied to the alkaline environs of cysts. Such a shock is experienced when melting snow or ice adds pure water to a basin, or when heavy run-off events like flash-floods deliver large volumes of low TDS water. Hatching begins, and continues, until dissolved materials reach about 1,000 ppm. TDS increases as salts in the soil dissolve and are mixed throughout the water by wind action, and as a consequence of evaporation. Where pools are subject to flash-floods, heavy rainstorms may repeatedly fill basins and create a hatch each time, or they may dilute the water that remains to also stimulate release of nauplii. In the latter case, two or more cohorts may swim phyllopod to phyllopod for the pool's duration.

In some cases, *Branchinecta mackini* may swim phyllopod to phyllopod with *B. lindahli*; more commonly they merely occupy the same "neighborhood". In either case, because of similar physiologies and perhaps presence one year and not another, competition between them may be a way of life (see p. 43 in the section on "Coexistence..."). The following life history traits are relevant to this possibility. As is typical of other species, clutch size increases with female length. Although variability is the name of the game, smaller females of *B. mackini* (10-16 mm) produce in the neighborhood of 2-50 cysts, these numbers being fewer than for *B. lindahli* of equivalent length. By about 20 mm, both species generate around 150 cysts per clutch. But as the length of *B. mackini* females increases above 22 mm, their brood pouch dramatically enlarges in volume allowing them to carry many more cysts (up to 450) than would be accounted for by a typical incremental addition to length (Maynard 1977). The upshot of these species' differences for *B. mackini*, dwelling in pools that last from 1.5-3.5 months, is a fecundity far greater than that of *B. lindahli* even though females of both species continue to produce clutches over their lifetime. For example, Maynard determined that *B. mackini* generated from 832-1,208 cysts (mean of 988) over a 77-day study period, but in another pool, during the same period, females of *B. lindahli* produced only one-third that number (mean of 326 cysts). The following year, in the same two habitats, but over a 33-day period, *B. mackini* females realized a mean of 545 cysts each, to 213 for *B. lindahli*. The relationship held! In the arena of competition, this means that longer-lasting pools favor *B. mackini*, but they lose out to *B. lindahli* in waters of short duration. Where these species coexist, a year of plentiful rain must favor *B. mackini*, while drought conditions would boost the other.

Because *Branchinecta mackini* is the major prey species of *B. gigas*, the two are often found together in playa habitats. In one Mojave Desert playa it was unexpectedly found with *Branchinecta coloradensis*, and in two others the cysts of both *B. mackini* and *Thamnocephalus platyurus* have been found, but coexistence is probably uncommon because the latter species hatches only during the heat of summer and early fall. In one instance, *B. mackini* was surprisingly found with *B. lynchi* in a roadside swale pool at the edge of the Pixley NWR in Tulare County.

Branchinecta gigas

(Map 5.6, p. 122; Fig. 4.1, p. 73)

Were you visiting with *Branchinecta mackini* in its western North America alkaline-basin homes, we believe you would gasp in amazement, or jump back in disbelief, should you net a 150-mm-long anostracan. We would! Still, our reaction would be tempered by the previous knowledge that this sasquatch of the fairy shrimp world, *Branchinecta gigas*, does exist, and almost always swims in the company of *B. mackini*. Well, perhaps "company" is not the most appropriate word to use, because *B. gigas*, as you know, is a predator, and *B. mackini* is its sushi of choice.

Because of this association, the distribution of *B. gigas* is similar to that just described for *B. mackini* (Map 5.11, p. 127). And because there is about a 1:40,000 ratio of the former with the latter (Brown & Carpelan 1971), the giant fairy shrimp lives in comparatively giant habitats. In other words, this predator's world must be expansive enough to house very large numbers of prey if its own population is to be big enough to assure survival. In California, this means that habitats of *Branchinecta gigas* are usually large pools associated with playas, or occasionally even the whole of the playa, and because such places must be of sufficient longevity for the completion of a life cycle requiring at least 40 days (Daborn 1975), this species is restricted to winter and spring (California collections are from late January to early May) in the Mojave and Great Basin deserts, from 700 m up to about 1,400 m. At the highest elevations, several aestival habitats are known, the largest being the 29-km-long playa called Middle Alkali Lake in Modoc County. At lower altitudes, all waters are unpredictable and seasonally astatic. You will note that this distribution and elevation range excludes the Central Valley.

Inasmuch as *Branchinecta gigas* occurs in many of the same alkaline habitats as *B. mackini*, the two obviously tolerate some of the same range of water chemistry. However, because the homes of the former are large, they are not as subject to extremes in concentration as the season progresses as are those in which *B. mackini* dwells alone. Brock (1988) reported that *B. gigas* disappeared at a TDS 25% less than when *B. mackini* populations went belly up a week or so later. The possibility exists that *B. gigas* did not survive because prey populations were rapidly declining, but Broch did not report population densities. Another scenario, this one consistent with ecological observations, is that *B. gigas*, in spite of being broadly tolerant of chemical and most physical conditions, cannot tolerate as high a temperature as *B. mackini*, for this giant predatory fairy shrimp has not been collected in waters warmer than 21°C. Whatever its limits might be, we must describe *B. gigas* as a species of relatively cool, if not cold, waters, which have high pH, alkalinity, and TDS (7.7-9.7, 300-960 ppm, 800-2,000 ppm, respectively; Eng *et al.* 1990). The occurrence of *B. gigas* in such a wide range of dissolved materials is at least partially explained by its ability to regulate body fluids hyperosmotically at low TDS, and survive high TDS by osmoconforming to a certain upper limit, one which is apparently less than for *B. mackini* (Broch 1988; Gonzalez *et al.* 1996).

In studies where both *B. gigas* and *B. mackini* were found together, they were noted to hatch at the same time. Therefore, Daborn (1975) assumed they utilize the same environmental clue as a dormancy breaker—a low TDS osmotic shock. How low the dissolved solids must be to stimulate hatching can vary between species and obviously does. Whatever the maximum stimulatory TDS value for *B. gigas* might be, we suggest it is lower than that for *B. mackini* (which approximates 1,000 ppm). We also propose that *B. gigas* has a lower maximum temperature for hatching, perhaps only 8°-10°C, whereas *B. mackini* will appear under considerably warmer conditions. Those willing to test these hypotheses can begin by considering the observations upon which they are based. First, *B. gigas* does not occur in summer pools even when its cysts are present and *B. mackini* has made its appearance (e.g., in Rabbit Dry Lake; Brown & Carpelan 1971). Second, *B. gigas* did not show up one year in a spring pool with an initial TDS considerably greater than usual, and yet *B. mackini* did (Broch 1988). And third, none of the authors we have cited reported more than one cohort of *B. gigas* per season, even though *B. mackini* can have several.

You may not be surprised to find that the giant fairy shrimp *Branchinecta gigas* produces giant cysts—the largest of any California anostracan (0.55 mm, Daborn 1975; 0.53 mm, Hill & Shepard in press). But because to now we have seen metanauplii emerging from large cysts, you may be surprised that nauplii, albeit large nauplii 0.90-1.10 mm in length, actually exit those of *B. gigas*. Daborn says the young feed on detritus, but upon reaching 7-10 mm they turn to carnivory and attain growth rates of 2.5-3.0 mm per day. Ovaries begin egg production when females are about 30 days old. At this age they are approximately 45 mm in length; given another 10-15 days, they average 60.6 mm but may exceed 70. Over this size range, 75-400 cysts are produced per clutch, the actual number being proportional to length of female, but the average will vary between years depending on available food. During one year of Daborn's study, females lived a maximum of 60 days, took 10-14 days to process each of their three clutches, and in the end demonstrated an average calculated fecundity of 630 cysts. Because the largest single clutch he recorded was 1,076 cysts for an 82.8 mm female, just imagine what the fecundity of the record-size 150-mm female might have been given her additional clutches over an extended life span...it must be mind boggling!

Fairy shrimps of warm-water pools which are low to moderate in dissolved solids, less predictable, and long-lived

Streptocephalus woottoni

(Map 5.3, p. 119; back cover)

Streptocephalus woottoni, first described by Eng *et al.* (1990), was given the name Riverside fairy shrimp because it was then known from but 5 pools about 45 km from the coast only in Western Riverside County. These included Skunk Hollow, the largest valley vernal pool remaining in all of southern California. Shortly thereafter, one of its refugia became the site of a gravel pit, the type locality was scraped for a housing development, and Skunk Hollow was slated to become a permanent lake surrounded by houses. Because of its limited occurrence, and further threats from construction, *Streptocephalus woottoni* was declared endangered by the Federal government in 1993. Thankfully, since that time several pools in Orange County, and some pool clusters on several mesa systems in western San Diego County, have been shown to house this rare beauty. Additionally, a couple of sites are now known on mesas immediately south of the international border in Baja California, Mexico. Even with these added locations, this species has one of the most restricted distributions among fairy shrimps endemic to the West Coast. With the exception of the remaining three in western Riverside County, all populations are within 15 km of the ocean over a north-south distance of about 140 km.

All pools benefiting *Streptocephalus woottoni* lie at elevations from 30-415 m in seasonal grasslands, some of which are interspersed among Chaparral or Coastal Sage Scrub vegetation. Several sites on the Chaparral-covered mesas immediately north of San Diego are considered San Diego Mesa Hardpan pools, while the two San Diego Mesa Claypan pools known to house this animal lie in the much finer grassland-supporting soils on the Otay Mesa east of the city (Keeler-Wolf *et al.* 1995). The remaining sites, including the pools on the coastal mesas near Oceanside, and Skunk Hollow of western Riverside County, have not yet been classified.

All of the swimming holes in which *Streptocephalus woottoni* plies its trade are seasonally astatic and are typically quite large, some exceeding 750 m^2. All have felt the impact of human activities, a number of them enlarged or deepened. They fill whenever late fall, winter, or spring rains generously bless the land, and because these basins are covered by 30 cm or more of water when full, they are comparatively long-lived, sometimes persisting into April or May (one record of early June). Such extended periods of wet soils usually allow the emergent rush *Eleocharis* to colonize the basins (Eng *et al.* 1990; Simovich & Fugate 1992). Although the water may be clear, more typically it is moderately turbid. Its very low TDS and alkalinity (means of 77 and 65 ppm, respectively) are corroborated by pH at neutral or just below (7.1-6.4) (Eng *et al.* 1990; Gonzalez *et al.* 1996; Moeur pers. comm.). Its appearance in waters with so few dissolved substances is explained in part by the fact it is an excellent hyperionic regulator, at least of Na^+, in very low TDS water. Once the environmental concentration reaches that of its blood, the animal dies. Additionally, *S. woottoni* can not tolerate 800-1,000 ppm of alkalinity for 24 hours. Although such amounts are much higher than any to which this species is naturally exposed, they are modest when compared to those with which several other southern California anostracans must deal every day (Gonzalez *et al.* 1996).

Very little is known about any biological aspect of this fairy shrimp. Among what we do know is that, in the laboratory, female *S. wootoni* will produce from 17 to 427 cysts over their lifetime (Simovich & Hathaway 1997). Cysts of *S. wootoni* will hatch, at least in certain situations, when placed in locales sometimes far from their natural pools. Clyde put some soil containing cysts in a newly-constructed basin on the Robert J. Bernard Biological Field Station of The Claremont Colleges in Claremont, and Denton added his aliquot of the same soil to a child's wading pool in San Antonio, Texas. When the rains came and conditions were appropriate (whatever those were), *S. wootoni* made its appearance. We assume that the cysts, with mean diameters of 0.27-0.31 mm (Hill & Shepard in press; Moeur pers. comm.) released nauplii, but neither of us checked this out.

Some of the pools in which *Streptocephalus wootoni* is found are known to contain *Branchinecta lindahli* or *B. sandiegonensis* as well. However, collections have shown that these species are usually mature or absent when *S. wootoni* is first taken. The prevailing explanation for this was that *S. wootoni* required a higher temperature for hatch and therefore did not emerge until later in the season (Eng *et al.* 1990; Simovich & Fugate 1992). Several years ago, John Moeur told us he believed that cysts actually hatch at temperatures in the vicinity of 10°C, but because development is so slow below 15°C, and the typical sampling net does not trap tiny animals, *S. wootoni* may merely be missed rather than be absent. Good reason for his reasoning, we thought, for on a fine January morning, when John took big *B. lindahli* and *B. sandiegonensis* from a mesa pool north of Oceanside, he noticed lots of dinky shrimps passing through the mesh of his net and back into their 11°C home. After 13 days, the precocious branchinectids were still there, but the baby shrimps had grown enough to show the undeniable traits of *Streptocephalus wootoni*. Demonstrating that such informed guesses (hypotheses) are sometimes correct, Hathaway and Simovich (1996) have now shown in lab experiments that *S. wootoni* hatches in 7-12 days if water temperatures are between 10-20°C, with some even appearing at 25°C. They also note that, depending on conditions, maturity of this relatively large fairy shrimp is attained in 48-56 days, and animals may remain as long as 120 days, although John Moeur (pers. comm.) has seen one population hang in there for 150 days. Such extended development and long tenure are certainly reasons for *S. wootoni* to reside in long-lived pools, some of which last into late spring when individuals may tolerate temperatures in excess of 25°C.

Just because these pools are described as "long-lived" does not mean they persist for extended periods each and every year. In fact, rainstorms in southern California are often highly problematic. If this animal hatched in a partially-filled basin, the water may disappear before *S. wootoni*'s long period of development is fulfilled, a situation that Simovich and Hathaway (1997) have observed up to 5 times in a year. It is not surprising then that many cysts do not respond to the first, second, or even third wetting. In fact, after three hydrations, a total of only 2.8% had hatched (range 0-13). This is the lowest reported hatching rate for any anostracan (Simovich & Hathaway 1997), but it certainly assures that cysts will remain for the blessed event of a filled pool.

The last of our observations is a colorful one. On a field trip to some deeper, near-coast pools, John Moeur dipped surface waters to show Clyde that here swam grayish male *S. wootoni*. By sweeping his net through the depths of the pool, John hauled in orange-red females. Denton and others believe the red is due to hemoglobin which better enables fertilized females to swim, undisturbed by amorous males, in areas of lower O_2, but this might not be the only scenario (you may wish to review again p. 29 in the section on "Color").

Please remember that if you contemplate MS or PhD research on this endangered animal, you will have to tackle some paper work for the USFWS; but don't fret, like the research itself, the chore is surmountable.

Fairy shrimps of warm-water pools which are moderate in dissolved solids, less predictable, and short-lived

Streptocephalus dorothae

(Map 5.3, p. 119)

Streptocephalus dorothae is the only one of the state's 23 species of Anostraca that has never been observed swimming in California pools. How do we know it's here? Well, Marie Simovich of the University of San Diego has a propensity for wandering around southern California and collecting dry soil from what appear to be pool basins. In the lab she subdivides each sample into containers which will be placed at several different temperatures, then follows that old directive "add water and stir". If cysts are present, they should hatch at appropriate temperatures. Hatchlings can then be raised to adulthood for identification. This approach does not require her to visit each and every pool during the limited time when adults are present.

Among Marie's dirt collections was a sample from Sunset Crossing in Banning. This scenic site, some 750 m in elevation, and along the route out of the L.A. Basin toward Palm Springs (or vise versa), lies at the crossing of the Southern Pacific Railroad tracks by Sunset Avenue. Here, in a rail-side ditch, *Streptocephalus dorothae* must swim in all its glory when runoff from rare summer thunderstorms fills its tub. Unless there was a mix-up in samples, we know it seeks asylum there, because back in the lab, sometime in 1992, out popped nauplii which grew to be adults of this animal when the soil was hydrated at 25°C.

Why did *Streptocephalus dorothae* settle down only in Banning? Where did it come from, and how did it get there? Good questions! No answers. However, thanks to Denton's work on the zoogeography of Arizona fairy shrimps (Belk 1977a), we may have a clue. *Streptocephalus dorothae* is reasonably widespread in Arizona, and the Southern Pacific Railroad connects Banning with the southwest of Arizona via Yuma. If it didn't get here via the suspected bird route, perhaps it rode the rails, or was smuggled in on the underbelly of some off-road vehicle. Perhaps. Maybe. No one knows. But such speculation may not be as wild as you might think. Maeda-Martinez *et al.* (1992) reported on another highly disjunct population of *S. dorothae*, the first record of this species in Mexico. It was found in a man-made roadside pool near La Paz at the southern tip of Baja California. The authors note that this too may be an example of "a recent man-assisted immigrant".

In an article that included some facts about the biology of *S. dorothae*, Denton (Belk 1977a) determined that hatching happens from 15-35°C, with 20° being about the best temperature and 35° not being very good at all. This information of course corroborates Marie's success at 25°C noted above. In addition, it supports the fact that *S. dorothae* is a summer species, a status also confirmed by its one-hour LD/50 of 40°C. Worthy of note is that such indulgence in high temperatures places this animal within one degree of the most heat-tolerant of Arizona Anostraca. Maeda-Martinez *et al.* (1992) supplemented Denton's information with the laboratory-derived observations that hatching begins to yield nauplii 24 hours after cysts are covered with water of 20-23°C, and continues for 48 hours. After 9 days, both sexes reach maturity at a length of about 8.5-

13.0 mm.

Man-made stock tanks or road-side ditches were the sites of 22 of Denton's 27 Arizona collections. Therefore, since this species apparently got as far as Banning, Sunset Crossing seems like appropriate harborage to us. How long water must remain in order for *S. dorothae* to complete its life cycle at summer temperatures is unknown, but, living as it does in unpredictable habitats, when it reproduces it does so with gusto. To illustrate, Denton patiently counted 846 cysts in the ovisac of a 20.5 cm-long female. Given such numbers it is no wonder that they are the smallest cysts (0.22 mm) of the Arizona fairy shrimps (Belk 1977a). Hill and Shepard's work (1997) demonstrates that, at 0.19 mm, they are among the smallest in California as well. The fact that so many cysts are generated, and that they seem to have a low hatching success at any one wetting (about 25%; Belk 1977a), bodes well for the survival of *Streptocephalus dorothae* in summer pools which at times may not last long enough for larvae to enjoy the fruits of growing to maturity.

Streptocephalus texanus

(Map 5.3, p. 119)

Collection records aren't much more numerous for *Streptocephalus texanus* than for our previous gem, but at least adults were encountered in the wild, though only at four locations in the extreme southeastern portion of California. The case of *S. texanus* is also a bit different because none of its populations made it very far into our state. One of its residences is in Imperial County, along the same Southern Pacific Railroad route that *S. dorothae* may have used and only 54 km from the Arizona border. The other three lie 2-38 km from the border in Imperial and Riverside counties. All sites are within 85 km of each other.

Being in the Colorado Desert, these locations are low in elevation (100-400 m) and particularly hot in summer when most of the year's meager rain descends on this parched land. In accord with such atmospheric timing, and the fact that *S. texanus* hatches at 15° and above but less than 32°C (Prophet 1963a; Horne 1967), we find it no surprise that the populations were discovered in June and early October. The waters were of course seasonally astatic, and included two granitic tanks, a pool in a dry stream channel (Eng *et al.* 1990), and what we suspect is a ditch along the railroad given its undescribed habitat 1.6 km south of Glamis. The only other shard of information concerning the California habitat of *S. texanus* is that the two tanks were turned green by algae.

Our knowledge of the biology of this streptocephalid comes from populations in other portions of its distribution, which extends eastward through Arizona (where it is also uncommon) and into the Great Plains (where it is common), then northward to Wyoming and Montana. *S. texanus* has been collected in water ranging from 13-37°C. It will tolerate the latter temperature for awhile, but will not survive at 10°C for more than 5 days (Prophet 1963c). The chemistry of the soup in which it swims seems to depend upon the state in which it resides. For example, in Kansas, Prophet (1963c) reported a range of pH from 4.7-9.5 (extremes which seem questionable), and alkalinities of 10-270 ppm (mean of 96 ppm; borderline low alkalinity). TDS (calculated from conductivity) averaged 177 ppm, or what we classify as low dissolved solids. By contrast, Horne (1967), working in southeastern Wyoming, recorded pH values of 7.5-8.5, alkalinities of 60-542 ppm, and TDS (from conductivity) of 73-16,455 ppm, the latter rising from 9,500 ppm over a three-day period because of evaporation. That's a lot of TDS! We suspect California habitats are moderate both in alkalinity and TDS. Our reasoning follows from the fact that summer rain is often of the cloudburst type, and, in this vegetation-sparse land, the rush of water will flush the tanks and washes, leaving behind pools of relatively fresh water. The other reason is that *Thamnocephalus platyurus*, a common co-inhabitant with streptocephalids elsewhere, and a resident of moderately alkaline water, was taken with *S. texanus* in two of its California locations.

If there are heat-loving adventurers amongst our readers who routinely follow reports of Colorado Desert weather, they might head for the hills and washes 11 days after a good downpour, for that is the time *Streptocephalus texanus* requires to hatch as a nauplius and grow to sexual maturity...at least in a laboratory at 20°C (Prophet 1963b). Let us know what you find, and supply a habitat description and water sample if possible.

Prophet's interest in the procreative details of anostracans that fight for space with Kansas wheat, led to the only information available concerning the reproductive potential of *S. texanus*. When a female first becomes mature, her initial clutch contains fewer than 25 cysts. Over a reproductive period of 11-27 days, females assemble 3-5 clutches with 3-654 cysts per clutch, resulting in the production of an average of 650 cysts, with the record being 1,635. That's a lot of cysts for an animal which hangs around for only 3-4 weeks, but perhaps not surprising inasmuch as the average cyst is only 0.21 mm in diameter (Hill & Shepard in press).

Thamnocephalus platyurus

(Map 5.11, p. 127)

The scientific handle for this animal means "shrub-headed flat-tail". The first part of the generic name comes from the highly divided frontal appendage on the male's head (Fig. 7.3, p.142), and the latter from the fusion of its cercopods with the telson to form a paddle-like posterior end (Fig. 7.1, p.140), both traits peculiar to this creature. In California, *Thamnocephalus platyurus* dwells in playas, a roadside ditch, a borrow pit, a tank, and several unspecified man-made places (Eng *et al.* 1990; Simovich & Fugate 1992) perhaps including stock ponds and road-side ditches which accounted for 90% of its residences in Arizona (Belk 1977a). Given its ability to live in non-natural pools, innumerable of which have been constructed throughout its distribution from Wyoming to Missouri to central Mexico, humans have obviously been responsible for a significant increase in the populations of *T. platyurus* (Belk 1977a).

The basins that house *Thamnocephalus platyurus* are located in the Mojave and Colorado Deserts at elevations of 1,235 m down to 65 m below sea level. These sites may fill in winter as well as summer and early fall. But because cysts will not hatch at water temperatures below about 17°, or at 32°C or above (Prophet 1963b; Belk 1977a), our "shrub-headed flat-tail" fairy shrimp is restricted to seasonally astatic pools, normally formed from mid-May to Mid-October, in Imperial, Riverside, San Bernardino, and San Diego counties. In these places it has been found twice with *Streptocephalus texanus*. It may occur with *Branchinecta mackini* also, since the cysts of both species have been removed together from several playas. Cysts of *T. platyurus* and *B. lindahli* are also present in the soil of one playa, but because they hatch at different temperatures, these two creatures would not swim together.

Except for a tank formed in a granitic outcrop and whose water clarity was reduced by algae, the habitats of *Thamnocephalus platyurus* are typically clay-bottomed and highly turbid. We also know from a California Academy of Sciences collection label that on September 12, 1955, 28°C and a pH of 7.5 were recorded as individuals of this species were snatched from the muddy waters of Bicycle Dry Lake on the Fort Irwin Military Reservation in San Bernardino County. Leaping forward a decade in time, Bob Brown scooped *T.*

platyurus from a 20x30-m borrow pit which he described as "not alkaline", along I-10, 40 km west of Blythe in Riverside County. This Arizona State University graduate student's observation was entirely feasible, for we note from information collected outside of California that *T. platyurus* is a species of low to moderate alkalinity (mean about 165 ppm) and TDS (mean of 320 ppm, from conductivity) (Horne 1967; Prophet 1963c; Belk unpubl.).

Hillyard and Vinegar (1972) collected adults from pools in Arizona and New Mexico whose temperatures reached 36.5°C and sometimes hovered near 35°C for much of the afternoon. From work in the laboratory, they noted that the animal tolerates temperatures as high as 38-40°C for at least an hour or two, but they died within 20 minutes at 44°C. Belk (1977a) determined a one-hour LD/50 of 41°C, and, at the other extreme of its temperature range, Prophet (1963a) observed that none survived 5 days at 10°C. The total of these facts shows that *T. platyurus* not only "loves" warm water but tolerates the highest temperatures of any North American anostracan. They appear to deal with about the widest pH range as well (4.7-9.2; Belk 1977b; Horne 1967; Prophet 1963c) if all data are to be believed.

The typical cyst is 0.27-0.30 mm in diameter (Hill & Shepard in press; Belk 1977a). This size, Denton says, is large for rainpool species, but because females of *T. platyurus* are more massive, and possess more spacious ovisacs than other anostracans on a length-for-length basis, they are able to carry as many big cysts as they do. For example, the ovisac of a 22.1-mm female contained 633. Of the other species studied which had individuals approximating this length, only females of *S. dorothae* carried more cysts (846); but remember, hers are perhaps the smallest amongst fairy shrimps. In any event, once expelled and dried, cysts begin to yield nauplii as early as 6 hours after wetting (Prophet 1963a) if temperatures are between 15-35°C, but they certainly hatch best from 20-25°C (Belk 1977a). How long it takes to reach maturity, and what the potential fecundity might be, are unknown, as are so many facets of this animal's life. In fact, this creature is so wonderfully strange in structure, and so tolerant of desert temperatures, it might well serve as a model for a number of biological questions worth asking about desert species. So, who will ask, then seek to solve them?

Fairy shrimps of cool- to warm-water pools which are great to impressive in dissolved solids, predictable, and temporary or permanent

Branchinecta campestris

(Map 5.12, p. 128; Fig. 5.1, p. 74)

Branchinecta campestris has been stumbled upon only once in California, the location being Soda Lake, 593 m in elevation, on the Carrizo Plain of San Luis Obispo County. The discoverer, biologist Larry Serpa of The Nature Conservancy, only said of his encounter that he ventured 6 m from shore (Belk & Serpa 1992). We use the word stumbled because of Clyde's close up and personal experience with Soda Lake's shore several years earlier. Under the supposed guidance of Robert Brown (who was without hip boots that day), Clyde waded out onto what had the appearance of an ice-covered bottom. You're right, it couldn't have been, and wasn't, ice. Rather, it was a thick crust of precipitated salts, and, in spite of his big feet, the crust didn't long support Clyde's 190 pounds. As he crunched through the salt and into the soft black ooze below, the stumbling began. In trying to pull one foot out, he pushed the other further into the quick-sand-like muck. When thigh-deep, his stumbling and progress decreased as panic increased. Yet somehow, "for the sake of science", and with "friend" Bob laughing in the background, he swept the water within arm's length for anostracans. The story's end was not Clyde's end, as you can tell by the prose in this book, but although the lake finally released him, it offered no anostracans as solace for its cruel joke.

In addition to *Branchinecta campestris*, Larry collected many brine shrimps in this very salty sump on April 20, 1991. Clyde's inability to sieve *Artemia* from the water was probably explained by the January date of his encounter, a time too early in the season for *Artemia*'s hatch to have yet occurred, but why *B. campestris* did not appear in his net goes unexplained.

Most of what is known about *Branchinecta campestris* and its abodes comes from research by Edmund Broch (1969) of Washington State University, and from a few tidbits of information supplied by James Lynch of the University of Washington (and *B. lynchi* fame) in his description of the species (Lynch 1960). From these sources we note, in the arid lands east of Washington's Cascades, *B. campestris* occurs in either seasonally or perennially astatic alkaline-saline waters at elevations from 335-730 m. This real estate lays claim to 9.5-10.0 pH readings, and possesses minimal turbidity because of high TDS (about 1,000-21,000 ppm). Around 95% of the major ions present are Na^+, Mg^{++}, and $SO4^=$ (Anderson 1958; Broch 1969). Recognizing that magnesium sulfate is what we call Epsom salts, the anostracans that spend their lives in this cathartic elixir must be very relaxed indeed! We wonder if they are equally serene in two Nebraska pools where Mg^{++} went unevaluated but HCO_3^- and $CO_3^=$ predominated at the expense of $SO_4^=$ (McCarraher 1970). We also wonder what the ionic proportions of these substances are in Soda Lake.

In Washington, Broch noted that a seasonally astatic habitat called Penley Lake alternated between standing water and frozen slush and ice throughout February. It wasn't until March 2, in 4°C water with a TDS of 1,080 ppm (from mOsm/L), that metanauplii of *B. campestris* appeared in large numbers. Broch (1969) intimates that water with a low TDS and a low temperature constitutes the hatching stimulus for its relatively large cysts (0.30-0.35 mm in diameter, Lynch 1960; 0.26 mm, Hill & Shepard in press). Broch also writes that individuals were mature about a month after hatching; the smallest female, 12 mm long, carried two cysts in her ovisac. By April 6, and at 10°C and about 15,000 ppm TDS, nauplii of *A. franciscana* made their debut. The population of *B. campestris* decreased in size during the three weeks of coexistence of the two species. By the time they disappeared (April 27), TDS equaled about 18,900 ppm and the temperature had reached 19°C. These data certainly parallel those of Lynch, who made all his Washington collections between late March and mid-June at water temperatures from 9-20°C. He did come across a Wyoming population on August 5, but this later date may be explained by its much higher locale (2,057 m) near Rawlins.

Broch concluded that the two species are able to divide common habitat on a seasonal basis because *B. campestris* is restricted to the cooler, lower-salinity phase, while *Artemia* carries on in warmer water and higher salt concentrations. Note that the upper limit of the "lower-salinity phase" in Brock's study is higher in dissolved solids than the typical habitat of any anostracan other than *Artemia*.

Also keep the foregoing facts in mind as you ponder what the yearly life cycle of *Branchinecta campestris* might be in central California. Regarding hatching temperatures, Clyde's experience does not help, for in his haste to extract his body from the mud of Soda Lake, measuring anything was far from his mind. He can say with assuredness though that the water was not icy cold. However, winter or spring rains and their runoff probably create a surface layer of dilute cool water that may activate the hatching process when it floods cysts lying in the desiccated shore of this seasonally astatic lake. Whatever the hatching clue might be, all we really know is that when collected on April 20 both anostracan species were mature, water in Soda Lake was 20°C, and both species swam together in a bucket of the brew for several days thereafter (Belk & Serpa 1992).

In his desire to show what it was about the physiology of *B. campestris* and *A. franciscana* that allowed them to divide a pool's tenure between them, Brock (1969) compared the total salt concentration of blood of *B. campestris* with that of their pool environment a number of times over the season. By so doing, he determined that individuals regulate hyperosmotically at lower concentrations of environmental TDS up to about 9,600 ppm (from mOsm/L). As their medium becomes further concentrated, the level of salts in their blood conforms to that of the environment. They tolerate this up to 21,000-25,500 ppm (from mOsm/L). Brock determined these latter figures in the laboratory by noting the concentrations at which all experimental animals died within 24 hours. That the level actually tolerated might be somewhat lower is suggested by the fact that he collected no individuals in concentrations greater than about 18,900 ppm TDS. Still, what is ecologically important here is that *B. campestris* can live in waters of greater TDS than any North American anostracan other than *Artemia franciscana* and *A. monica*. You will remember that the ability of *Artemia* to regulate its blood hypo-osmotically allows it the freedom of swimming unmolested (by invertebrates) in extraordinarily concentrated brines.

Most of the time *B. campestris* swims alone, but not uncommonly it occurs with *Artemia franciscana*, as in Soda Lake. Given their preference for alkaline water, no one should be surprised that *Branchinecta mackini* and *B. lindahli* have also been recorded in the same pool at the same time as *B. campestris*.

Artemia franciscana

(Map 5.12, p. 128)

Most kids who read comic books, or anyone interested in the aquatic creatures sold in pet shops, know of "sea monkeys". Buy a packet of "eggs" (cysts), add a pinch of these to some salty chloride-laden water (sea water does just fine), and presto, instant life! "Instant" means be patient for a day or two, at which time tiny nauplius larvae of the brine shrimp *Artemia franciscana* will appear, swimming jerkily, before your very eyes. As they mature, and males begin to chase females, you will see them looping through the water, perhaps suggesting a monkey swinging from tree branches, and thus, we suppose, their name.

Throughout this book you have seen us refer to anostracan species with both their generic and specific names – with an exception, and that is *Artemia*. For this beast, sometimes only the generic name is used. Until "recently" much of the literature referred to these creatures as *Artemia salina*, or frequently merely as *Artemia*. The reason is simple; the explanation could be long and involved. Suffice it to say that *Artemia* dwells in a great array of highly concentrated chemical habitats almost always high in Cl^- (Cole & Brown 1967), and a host of physiological differences has developed among populations to deal with these and other environmental exigencies (e.g., Bowen *et al.* 1988). However, little anatomical variation has appeared even among those that are now accepted as distinct species. So, for example, it is all but impossible to distinguish structurally between the two California species *A. franciscana* and *A. monica*. In order to make distinctions between populations, one must inquire into the sexual compatibility of their members (do they mate and produce fertile offspring?), sexual preferences (do they reproduce without males, by producing cysts, or by giving life birth?), genetic similarity (or lack of same), and their tolerance of brines of different chemical compositions. Obviously none of these chores is accomplished in a few minutes under optical magnification, nor by those unschooled in such matters – like your authors!

Artemia, then, is a complex of species, incipient species, physiological races, call them what you will. Some of the intricate matters concerning population differences have been worked out by the likes of Sarane Bowen, a professor at CSU San Francisco and world-expert on the subject. But what species or population was utilized in many of the works published over the years is conjectural by her and other experts, and unknown to the rest of us. Now you know "the rest of the story".

Thanks to Sarane and her coworkers (e.g., Bowen *et al.* 1985) we are reasonably sure that California populations of *Artemia*, except the one living in Mono Lake, are *Artemia franciscana*. This species was originally described from specimens collected in a saltern (salt-evaporating pond) near Redwood City on the shores of San Francisco Bay. There are various salterns around the Bay, and *A. franciscana* occurs in all. Its presence has also been noted at Monterey and San Diego bays' saltworks. Whether these populations are natural, or were introduced to benefit the process of evaporation in salt extraction (see p. 8 in the section on "What good are fairy shrimps?"), is not known. Because *Artemia* is restricted to highly saline waters, its distribution in inland California is spotty, limited to approximately the central third of the state, and from near sea level to 1,495 m. In the Mojave Desert, most playa lakes are high in alkali minerals but low in chloride and are thus unsuitable for *Artemia*. However, in a few playas with elevated chloride, there resides *A. franciscana*. Populations are known from Koehn Dry Lake in Kern County, and from South Panamint Dry Lake, Owens Lake, and Deep Springs Lake in Inyo County. In the arid southern half of the Central Valley, our saline friend has shown up in Contra Costa County, near Livermore in Alameda County, on the Kesterson NWR in Merced County, and close to Lemoore (Kings County), the latter site appearing to be excavated to collect saline run-off. In the Central Coast Mountains Region, at its interface with the southern Central Valley, *Artemia franciscana* swims in Soda Lake, in a number of pools in run-off channels that empty into the lake, and in several sag ponds along the San Andreas Fault about 30 km to the southeast in San Luis Obispo County and just over the border in Kern County.

All sites just mentioned are seasonally or perennially astatic hypersaline playas, lakes, and pools, or human-constructed sumps or salterns. Natural habitats among these fill with winter and spring rains; the sumps and salterns are undoubtedly flooded by rain, or whenever economic reality dictates. Although the animals' briny bath may be full, cysts do not hatch until temperature reaches 9-10°C (Broch 1969; Relyea 1937); the optimal range is 15-30°C (Bowen *et al.* 1984). This means that in some of the smaller bodies of water which heat up hurriedly, *Artemia* has been collected as early as mid-January; in larger basins, and at higher elevations, its presence is delayed. Collections from these larger sites have been so spotty that we do not know when individuals first appeared and when they disappeared, but animals have been taken as late as the end of July. No problem; just because summer means high temperatures doesn't mean *A. franciscana* can't "hack it", for this hardy animal is known to tolerate at least 37°C (Galen 1969). Because evaporation at this number of degrees is great, so may be the salinity of what began as already high-TDS water, but no problem here either for this anostracan can even handle saturated brines.

In California, this amazing creature has been removed from natural brines of about 1.0-4.9 times the concentration of sea water, namely 34,914-172,000 ppm of dissolved material (Eng *et al.* 1990), the latter being enough to make all multicellular life, except *Artemia* and the brine fly, gag! In coastal salterns the milieu is, of course, some concentration of sea water and, therefore, high in Na^+ and Cl^- and low in alkalinity (HCO_3^- and $CO_3^=$). Little information is available concerning the chemical makeup of its inland California habitats, although from what is known Cl^- dominates (6,420-34,000 ppm), and alkalinity is a minor player (74-1,307 ppm. pH ranges from 7.4-9.1 (Eng *et al.* 1990). We remind you that at TDS levels much above 3,000 ppm, clay particles precipitate to yield clear, though possibly tea-colored, water, a description applicable to California's habitats harboring *Artemia franciscana*.

How adults of *Artemia* deal with such wide osmotic and ionic variations, and extreme levels of salt, is a story told in the classic papers by Croghan (1958a,b,c,d,e; see p. 18 in section on "Water, salts, and liquid wastes: their regulation"). Obviously, nauplii face challenges similar to those of adults, and thus have the same physiological abilities (Russler & Mangos 1978; Conte 1984). Suffice it to say here that all life stages of *Artemia* are hyperosmotic regulators at lower environmental salt concentrations, an ability which allows them to acclimate slowly to solutions with TDS of only 8% that of sea water (2,600 ppm; Croghan 1958b) even though they do not reproduce in them. Then, with greater capability than any other multicellular species except perhaps the brine fly, individuals can hypo-osmotically regulate their body fluids so ably that they can dwell in unbelievably concentrated brines – perhaps as high as 330,000 ppm (almost 9.5 times the concentration of sea water; Bowen *et al.* 1984), a figure twice that in our field data, but one which must commonly occur in the final aquatic stages of salterns.

Artemia presents special difficulties in describing or interpreting its biology. Because its populations live in, and have become adapted to, a variety of conditions which are so wide and extreme, it behooves us to know not only from which population the studied batch of organisms comes, but what their environmental background has been. Seldom is much of this known, although if they are raised from cysts in the lab, a simple and common practice, at least conditions under which they grow up can be prescribed and described. In any event, consider the comments that follow to be generalizations, because they are accumulated from laboratory and field, and from a mix of populations often facing quite different environmental realities.

We have mentioned that cysts begin to hatch around 10°C. But we have not mentioned that those cysts are the smallest produced by California anostracans, averaging 17.9 mm (minimum 12.1, maximum 22.6 mm; Hill & Shepard in press). At around 15°, three days of wetting are necessary before nauplii appear. At the comfortable temperature of 20°C, nauplii emerge in two days, while they can be hurried from their cysts in one at 30°C (Galen 1969). Bowen *et al.* (1984) describe populations in San Francisco Bay salterns as hatching best at 15-30°C while those from Fallon, Nevada, hatch optimally between 10-20°C, a difference that makes ecological sense (described below), and illustrates the fact that the biology of this animal cannot be detailed with a few average measurements.

In a parallel Mediterranean situation, Browne (1993) noted that "*Artemia tunisiana* tolerates cold quite well and produces mainly cysts, so it is well adapted to conditions found in ephemeral inland lakes, which are usually filled with water during only the colder winter months ". Browne goes on to say that forms giving live birth and tolerating warm water are more suited to salterns which are maintained for much of the year. *Artemia franciscana*, hatched and reared in the laboratory from San Francisco cysts, apparently has a phyllopod in both camps. To oversimplify the complex work and sometimes seemingly contradictory findings of Berthélémy-Okazaki and Hedgecock (1987), at temperatures of 16-22°C and photoperiods of 12 hours or less of light, 68-99% of females produce cysts (the remainder give birth to live nauplii), but only 10% do so when days are long or light is continuous. Ah ha, photoperiod is very important, but its influence is lessened by higher temperatures, in which case 50% of females produce cysts irrespective of day length. To show you how complicated things can get, we'll add the following interesting information then move on to another subject. Under 9 hours of light (short photoperiod) and 19-23°C, an average of 67% of females produced live young in their first clutch. However, hidden within this figure is the fact that if they matured rapidly (15-18 days), more than 85% of females had live births, but less than 50% did so if maturation was delayed (20-27 days). In their second and successive clutches, only 15-35% released live young; the remaining percentages, of course, belonged to cyst producers. As you poke through these details, you will see they make sense ecologically. By initially generating a preponderance of live young, the population gets off to a fast start. But, as the season advances and the habitat shrinks, possibly soon to evaporate to oblivion, the situation demands that females get on with cyst production!

In their paper, Berthélémy-Okazaki and Hedgecock (1987) show in graph form that females mature in 15-32 days when temperatures approximate 20°C and the brine is 30,000 ppm. Weisz (1946) reported 32 days for the attainment of maturity at this temperature and salinity, but only 22 days at 115,000 ppm, suggesting that the time to attainment of *Artemia*'s sex life is inversely dependent on the salt concentration of the environment in which its lot is cast. But then along comes Gilchrist (1960) who claims that the extent to which growth is determined by salinity varies with sex, and we would add probably with the source of cysts as well.

Once mature, how big can *A. franciscana* become and just how long can it live? Relyea (1937) said that adult males from the Great Salt Lake grow to 8-10 mm in length, while females measure in at 10-12 mm; that's pretty small compared to most anostracans! Browne and Salle (1984) reported that the mean maximum life-span of two California populations was 92 days (13 weeks). What the "normal" average might be is undoubtedly lost in the "noise" of all the variation that exists.

Browne (1980) confided that an *Artemia* female produces a clutch every 4-6 days, and a total of 10-19 clutches (maximum of 25) over her lifespan. Given that each clutch contains from 78-111 cysts (the record of 300 seems a terrible load for an animal of *Artemia*'s size), total fecundity per female could approximate 1,500-2,000 potential offspring. In places like the Great Salt Lake, there may be so many hemoglobin-laden *Artemia* crammed together that they turn the water red. In such a circumstance, if each female churned out even a portion of the above number of cysts that when extruded from the ovisac float on the high-density saline water (Bowen *et al.* 1984) and get blown to shore, it is no wonder that, during the early days of the *Artemia*-cyst industry, shovels were used to collect these little jewels from windrows at water's edge. By the way, related to this thought is a neat bit of trivia. Given there are about 330,000 cysts per gram (9.25 million per ounce; Hill 1995), can you imagine how many there are in a shovel full? In a ton? In the 2,200 tons now harvested annually (Williams 1995; see also p. 8 in "What good are fairy shrimps?")? That number must approach the national debt!

Anyhow, all good things must come to an end, and Relyea (1937) describes an end to the yearly reproductive escapades of Great Salt Lake adults when they die as temperatures drop below 6°C in the fall.

In California, *Artemia franciscana* has been seen in the same place and at the same time with only one other anostracan – and only once. Given its briny living standards, that fact is not surprising. The one species was *Branchinecta campestris*, and that one place was Soda Lake in San Luis Obispo County. The fact that these two phyllopodous philanderers have been netted together there only once is not particularly surprising either, because Soda Lake is apparently not oft collected. To review the elaborate details of their co-occurrence, refer to the section on *B. campestris* (pp. 109-111).

Artemia monica

(Map 5.12, p. 128)

Artemia monica is a California endemic found only in one place, Mono Lake in Mono County. That sounds pretty restrictive, and so it is, yet we have stated that *Linderiella santarosae* is the California-endemic anostracan most limited in distribution even though it is found in several pools. The difference, of course, lies in land area covered. Mono Lake, even though smaller than it was in the forties because of water diversion from its basin by the City of Los Angeles, is still some 25 times greater in surface area than the entire tract of pools in which *L. santarosae* dwells.

Certainly the contents of this oldest lake in North America (500,000 years; Lajoie 1968) began as fresh water, but with the continual addition of small amounts of salts carried to it in run-off, and the fact that over much of Mono Lake's life the only way water left was via evaporation, slowly, very slowly, its dissolved materials rose in concentration. Somewhere in time, after it became sufficiently saline, some cysts were introduced, most probably from a population of *Artemia franciscana*. As the water continued to concentrate, and the saline character of the lake became unique, so did the biology of its population of *Artemia* (Bowen *et al.* 1984, 1985).

About 50 m deep, Mono Lake contains such a large volume of water that fluctuations in its physical and chemical nature are minimized. Thus, the population that evolved into *Artemia monica* has not had to deal with the environmental extremes faced by other *Artemia* stocks. Yearly, water temperatures throughout the lake's depth range from 4-24°C (Lenz 1980). In the days when Mark Twain took a boat ride on its surface, TDS was probably around 50,000 ppm. When David Mason was doing the first intensive aquatic study of the lake in the mid-sixties, he found TDS of its clear waters to be 76,000 ppm, Cl^- was 17,500 ppm, and pH stood at 9.7 (Mason 1967). By 1988, TDS had risen to 93,600 ppm and Cl^- had reached 19,500 ppm (David Herbst pers. comm.). These figures are certainly not out of the ordinary for *Artemia* habitats. So what's the big deal? It turns out that the alkalinity recorded at Mono Lake is far and away greater than anything known from California (19,500 ppm in Mason's day, 36,700 ppm in 1988), or anywhere for that matter except Jesse Lake in those old sand hills of Nebraska.

One reason for the uniqueness of *Artemia monica*, then, is that it must live in brines which have a high ratio of alkalinity to chloride. Given this reality, the species cannot survive in the salt solutions that support *A. franciscana*. The reverse is also true, that is, *A. franciscana* dies when subjected to *A. monica*'s highly alkaline water. Obviously the physiologies of these two, as blueprinted by their genetics, have become quite different.

Even though the ionic composition of water in Mono Lake differs so considerably from the variations on the theme of those inhabited by *A. franciscana*, we doubt you will be surprised to read here that the Mono Lake brine shrimp, being an *Artemia*, can regulate its blood concentration hypo-osmotically over quite a range (at least from 50,000-146,000 ppm TDS). Below 50,000 ppm, males show signs of regulatory stress. From 146,000-189,000 ppm, still "a breeze" for *A. franciscana*, both sexes of *A. monica*, males particularly, exhibit signs of regulatory loss, verified by an increased number of deaths (Herbst & Dana 1980). Experiments aimed at studying hyperosmotic regulatory abilities of *Artemia monica* have not been undertaken. However, given the above comments that males show signs of regulatory stress below 50,000 ppm TDS, Mono Lake brine shrimps apparently do not possess this skill.

The cyst of *A. monica* falls within the same size range as that of *A. franciscana* (mean of 0.19 mm, Hill & Shepard in press). But that's about where the similarity ends. Unlike those of the latter, *A. monica*'s cysts sink when released from the ovisac, do not require a period of desiccation, but do need 1-3 months of cold-water incubation before hatching, in March, at an optimal temperature of 5°C (Bowen *et al.* 1984). Gravid females begin to appear in May which suggests that about two months are required to attain maturity during the low temperatures of spring. When reared at 20°C (which approximates summer surface temperatures), only 30-40 days are needed. Females produce live young throughout May, but switch to cyst production in June). The summer population is usually smaller than the spring one, but the actual size depends on food supply and salinity (Dana & Lenz 1986). Individuals have been seen plying Mono Lake's water throughout the year but their numbers are severely reduced in winter (Lenz 1980). Even though Mason (1963) measured shrimps from 7.9-11.1 mm in length (similar to *A. franciscana*), and clutch size has been determined to vary directly with animal length and inversely with salinity, from data at hand it appears that *A. monica* produces about half the number of offspring per clutch (in the range of 40-65) as does *A. franciscana* (Dana & Lenz 1986). No one has calculated *A. monica's* fecundity, however, we suspect that females have the potential to churn out clutches until their genetically allotted time runs out (about 65 days; Dana and Lenz 1986), since they live in a permanent habitat, or until they serve as a tasty treat in the diet of the myriad of breeding and migratory birds that spend time plying the salty surface of Mono Lake (Herbst & Dana 1980).

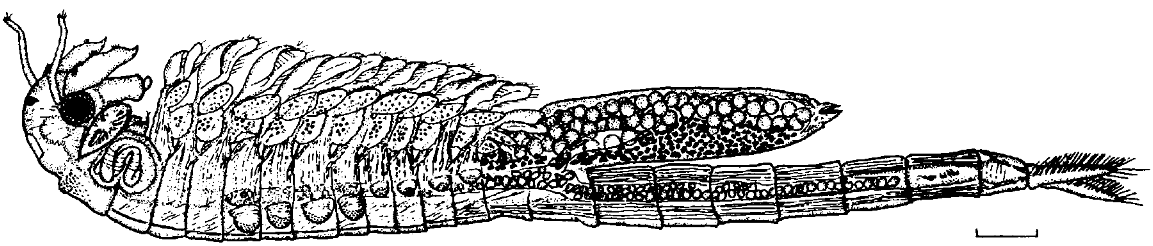


Fig. 5.3. Female of *Branchinecta lindahli* from Lynch (1964); reprinted courtesy of *The American Midland Naturalist* (scale = 1 mm).

Map 5.1. Counties of California.