life stage and species (Mertens *et al.* 1991). As appendages return forward from a beat, a low pressure is created between them causing water to flow in (be "sucked" in) with its dead particles, and living organisms too if they are unable to swim against the flow. When the phyllopodia beat once more, whether in graceful swimming or bottom scraping, increased pressure forces water through the setal meshwork and particles too large to pass through its pores are sieved out, whether living or dead, plant, animal, or mineral, nutritious or not. These particles are moved to a **food groove** between the bases of the phyllopodia, then passed along to the jaws and mouth by specialized spiny lobes at the base of each appendage. For an excellent discussion of anostracan feeding mechanisms, see Fryer (1983).

For those of you who enjoy history, it may be of interest to know that until just recently a fairy shrimp's **two fused genital segments** were thought to be part of its abdomen because, like that portion of the body, they lacked phyllopodia. However, certain perceptive and dogged scientists (e.g., Walossek 1993), noting that sex ducts of related fossil and living branchiopods all open on phyllopodia, that the embryology of the genital segments is more similar to thoracic than abdominal development, and that the penes of the male are actually derived through evolutionary modification of a pair of phyllopodia, have finally persuaded skeptics that the fused genital region truly belongs to the thorax! That issue settled, we can now rest in peace with the notion that the posterior portion of the thorax is the focal point for the reproductive organs and their accessory internal and external structures.

Internally, **ovaries** and **testes** are paired, blind tubules that lie alongside the gut, mainly in the abdomen, but in some species an anterior branch extends further into the thorax as well. The male's two **penes** protrude from the ventral surface of the fused 12th and 13th segments of the thorax (Fig. 1.2, p. 2). Yes, you read correctly, males actually have two penes. Each lateral testis empties through only the penis on its side of the body.

In females, **oviducts** extend from the ovaries and enlarge at their distal ends into what are called **lateral pouches**. These join one even larger structure called an **ovisac** which also receives ducts from several **shell glands**. The ovisac expands within the **brood pouch** which is a centrally placed and posteriorly directed protrusion from the ventral body wall of the fused genital segments (Fig. 1.3, p. 3). The opening of the ovisac to the outside is the female's **genital pore**, the site that male sexual behavior is aimed at entering for insemination. Rather detailed illustrations of this system can be seen in a paper by Brendonck (1991).

The **head**, the most anterior portion of the body, is situated immediately in front of the thorax, and bears the **mandibles** (jaws) and other tools. Rotating action of the mandibles helps crush and push food into the mouth (Fryer 1966). The grub is moved to the teeth-like mandibles from the thoracic food groove by two pairs of small head appendages located immediately behind the mandibles, the **maxillae** (Manton 1977). Unlike the teeth of humans and your pet goldfish, but similar to a grasshopper or lobster, a fairy shrimp's mandibles are not within its mouth cavity, rather they flank and ultimately cover the mouth. Immediately anterior to the mouth, and overhanging the mandibles, is a lobe or mound called the labrum, or "upper lip", which effectively prevents leakage from between the mandibles and serves as a backstop for food that might otherwise be pushed further forward. This device thus assures that mandibular action gets all of the food into the mouth. No messy face here!

More forward yet are one pair of large,

stalked, **compound eyes** and two pairs of antennae, referred to as **antennules** and **antennae** (Fig. 1.3, p. 3). In males, the antennae are large, and possess a variety of processes and appendages, as well as ridges and mounds which may be ornamented with spines or denticles (check out the many examples on pages 143-165). Because antennal shape and ornamentation apparently aid a female in choosing a mature mate, such features differ from species to species (Belk 1991a). As might be imagined, the crafty fairy shrimp taxonomists have learned to use the male antennae, with their bumps, processes, and acne-like ornamentations, as the main distinguishing characteristics of species.

The **abdomen** is continuous with the posterior end of the thorax and bears at its terminus a pair of setae-fringed, fluke-like **cercopods** (Fig. 7.1, p. 140). These cercopods are used in concert with abdominal musculature in turns as well as in rapid escape locomotion much as beavers, whales, or lobsters would employ their tails and bodies. Should you touch a cercopod you may stimulate a flurry of such behavior, so it seems these structures serve a rear-guard sensory function as well.

Circulatory system

So far our discussion has dealt with fairy shrimp parts that "meet the eye". But how about its "innards"? We begin with the circulatory system, a fascinating component of internal structure. Unlike your closed system of blood vessels, the fairy shrimp has an **open circulatory system** to transport oxygen, digested food materials, hormones, and wastes through its body. The system is said to be "open" because the long, dorsal, tubular heart pumps blood anteriorly into the head region, whence it flows posteriorly through body spaces largely under the force of muscles contracting for other body functions. In other words, there are no arteries, capillaries, or veins, and the heart is not the only propulsive force (Greene 1924). Blood thus surrounds and bathes all body organs, flows out into all appendages where the majority of oxygen uptake from the environment is thought to occur, then generally moves posteriorly where it re-enters the heart via valved openings called ostia.

If you want to see a thing of beauty and perpetual motion, isolate a fairy shrimp in a small volume of water (a clear-plastic box 2-4 cm across works fine) and observe it carefully with a magnifying glass or dissecting microscope. If you can take your eyes off the continuous motion of appendages and look inside through the thin, semitransparent exoskeleton, you will not see defined body spaces filled with blood. What you will observe above the dark, food-filled gut is the dorsal, elongate heart pumping rhythmically and continuously to the beat of its unseen metronome – the heart pacemaker.

The blood, called **hemolymph**, is usually colorless, and it contains cells, the movement of which will allow you to trace the general direction of blood flow (Greene 1924). At times the hemolymph may contain dissolved, not cell-bound, **hemoglobin**, which of course is a red, iron-based respiratory pigment. Because the exoskeleton is so thin, this internal color makes the animal appear reddish. Under conditions of plentiful oxygen hemoglobin is absent (why make it if you don't have to?), but in those species having the genetic ability, hemoglobin appears to be synthesized in response to low environmental oxygen levels, allowing the animals to increase the supply of oxygen carried to their tissues.

Oxygen: its procurement and regulation

Oxygen (O_2) is required for metabolic processes from which energy is released to accomplish bodily work like locomotion, growth, egg and sperm production, and all that sexual activity we will speak about with biological frankness later in the chapter. Aquatic creatures must not only take in sufficient O_2, but most must also maintain the rate of its intake, though some species may possibly just "tough it out" in the face of a pool's decreasing supply; and a reality of pool life is that the quantity of O_2 does rise and fall, sometimes drastically, even within a few hours. Oxygen, when in its greatest concentration in water, is present in minuscule amounts compared to air. While the atmosphere contains approximately 200,000 parts of O_2 for every million parts of air (ppm), water, at its maximum, is capable of dissolving only slightly less than 15 ppm, and the amount actually available dwindles from there! Scary, eh?

There is importance as well as fascination in understanding the physical and biological relationship between the amount of O_2 in an aquatic environment, and the latter's temperature, salinity, and susceptibility to being mixed by wind. Remember, these factors are among the most conspicuous and significant actors in the dramatically-changing conditions typical of temporary waters. Before we mention the effects of these environmental agents on species, an enthusiastic discourse on their interrelatedness seems warranted.

Most temporary waters are small in volume and possess large surface areas compared to their depths. These characteristics generally assure that the water is well mixed by wind and thus supplied with oxygen throughout. During winter and spring the atmosphere is cool and breezy, so the pools mirror these amiable conditions, and O_2 is seldom in short supply. However, warm, calm days in the environs of temporary waters are not uncommon, and, as the water heats at such times, its capacity to dissolve oxygen drops. Warming water also speeds up evaporation, consequences of which are the concentration of its dissolved salts and, therefore, the further reduction of its O_2 content – strikingly so in briny waters. The big problem is that in the face of these reductions the consumption of oxygen by pool creatures increases dramatically as their metabolic rate is elevated by higher temperatures. To make matters worse, atmospheric oxygen is not redistributed to the pool's volume at times of atmospheric calm. Should the habitat contain phytoplankton or submerged aquatic vegetation, O_2 is added to the water by photosynthesis during daylight hours; but at night all of the pool organisms, plants included, continue to consume the absolutely necessary but limited supply of dissolved oxygen. As a consequence, O_2 may decrease dramatically until the time "ol' Sol" begins again to brighten the morning sky.

Having said all of that, we must now advise that not much is known about how fairy shrimps gain their oxygen and cope with drastically changing concentrations. Of course most aquatic animals obtain O_2 from the environment via gills. Where then are the gills of fairy shrimps? We have already described how the phyllopod appendage is composed of several leaf-like lobes, one of which has been referred to as a gill. Undoubtedly these lobes serve in the intake of oxygen, but their combined surface-area is probably too small to account for the total volume of O_2 needed by a fairy shrimp given the energetic demands of constant swimming.

Large enough or not, Modlin (1985) suggests that species with a propensity for greater activity have larger gills than those which are less active. For example, he observed that *Eubranchipus holmani*, a constantly swimming, plankton-eating species, has gills 1.5 times the size of those of *E. neglectus* (misidentified as *E. vernalis*), which he suggests has a less energetic life-style because it sometimes feeds by scraping the bottom sediments and occasionally rests on the bottom while there.

Whatever the case, we believe that the surface area of the gills is still too small for sufficient O_2 intake when the fairy shrimp is faced, because of increasing temperature, with an escalating metabolic rate and scarce environmental oxygen supplies. Why do we say this with such authority? Well, partly because of some limited research on fairy shrimps, partly because of your first author's research on aquatic insects, and partly because of the characteristics that define a respiratory surface. Read on for the arguments.

Intuition tells us that a **large surface area** can allow more oxygen to pass through it per unit of time than a smaller one. The hemolymph within the **circulatory system** then courses through the gill to carry off the O_2 that enters. **Thinness** is a virtue because the distance that oxygen must travel from the environment outside to the hemolymph inside is minimized. Obviously the longer it takes to move O_2, via diffusion, to the circulatory system, the less the total amount that is transported to the tissues in a given period of time. And of course too much cellular bulk in a gill means that much of the O_2 would be used within the tissues and not be carried away at all. Oxygen needs to dissolve in water before it can pass through a respiratory surface; therefore, such surfaces must be **moist**. Maintaining moistness is not thought of as a problem for gills, of course, because only aquatic organisms possess them. However, it helps explain why gills do not function when they dry out. Finally, water containing the needed O_2 must be constantly renewed next to the intake surface, for with use the surrounding supplies dwindle into insufficiency. The renewal process is called **ventilation**, and may be actively accomplished by the animal, or passively provided by the environment flowing over the organism. When you breathe, you ventilate your lungs. The fairy shrimp breathes by beating its phyllopodia, a process which not only moves our favored creature through the water, but also passes water over its respiratory surfaces thus ventilating them as well.

Given these criteria for respiratory surfaces, one can see why a particularly blood-rich portion of an appendage might be considered a gill. But take note, as did Martin (1992), that the rest of the phyllopod is also thin, as is the exoskeleton and epidermis of the remainder of the body, particularly the thorax and abdomen; he concluded, therefore, that these surfaces undoubtedly also play a role in the uptake of oxygen. We confidently agree with Martin's conclusion for two reasons. Firstly, Gilchrist (1958, 1960) seems to have demonstrated that the male of *Artemia franciscana*, whose second antennae have very large blade-like portions, uses these surfaces for O_2 intake. Secondly, Eriksen (1986) and Eriksen and Moeur (1990) have shown that, for several aquatic insects, the general body surface, particularly the abdomen, is vitally supplemental to the gills in O_2 uptake.

No matter the extent of the respiratory surfaces, the ability to maintain a constant intake of oxygen through them in the face of a dwindling supply (**respiratory regulation**) is particularly important for organisms which dwell in habitats whose O_2 supply varies greatly throughout the day. If you wonder why regulation is so important, consider what would happen to your activity if your metabolism was yanked around by a drastically changing environmental O_2 supply because you could not increase or decrease your breathing rate in order to keep oxygen intake steady. Our guess is that you, and any other beast, would be at a serious disadvantage when in competition with creatures who, like Energizer batteries, "just keep going , and going, and going" at a constant rate.

The only anostracans whose O_2 intake have been determined over a range of environmental oxygen concentrations are *Branchinecta mackini*, the alkali fairy shrimp (Eriksen & Brown 1980b), and, yes, you guessed it, the brine shrimp, *Artemia franciscana* (Gilchrist 1954). Using these species as suggestive models, we can probably pronounce with some "ball park" assurance that fairy shrimps are respiratory regulators. You and the authors of this book regulate O_2 intake by changing the rate of our breathing as our needs vary. Fairy shrimps undoubtedly accomplish the same effect by varying the beating rate of their appendages. As useful as this ability might be over a range of oxygen concentrations, it has its limits at some genetically-determined low critical-level of oxygen. The particular level is "critical" because below that amount the animal is unable to obtain enough O_2 to sustain its metabolism and thus its necessary activities. For adult *B. mackini* tested at 12°C, this low critical-level lies between 1.4-2.9 ppm of oxygen, depending on the exigencies of the habitat to which the population is acclimated. Good ol' *Artemia* also falls within this range, 2.3 ppm, even though its test temperature was about 10°C higher (23.5°C). At lower temperatures, the critical level is undoubtedly lowered as well because the metabolic rate, thus the demand for O_2, declines. However, when water is below 10-15°C, low oxygen is seldom encountered.

To the contrary, when temperatures are higher, say 20° or 30°C, O_2 is more scarce and metabolic rate is considerably elevated, so the low critical-level of oxygen will undoubtedly be significantly higher. Perhaps this conflict of increasing temperature, metabolic rate, and O_2 need, in the face of a dwindling supply, is one of the reasons that most California fairy shrimp species appear during winter and spring. Among the 23 kinds of anostracans that swim in California's wet spots, only 5 might be considered "warm-water types", that is, fairy shrimps that will not hatch until water temperature exceeds about 15-17°C and which can do well as adults in temperatures exceeding 25-30°C.

If indeed cool- or cold-water fairy shrimps do not usually have a problem with the environmental O_2 supply, how is it that the few species whose little lights shine in warmer water succeed in what must be significantly lower O_2 concentrations? Once more there are few studies and therefore little in the way of definitive answers, but in reaching for at least some educated guesses to pass along to our readers, we return again to *Artemia* the brine shrimp, *Branchinecta mackini* the alkali fairy shrimp, and a warm-pool anostracan, the intriguing beavertail fairy shrimp *Thamnocephalus platyurus*, to serve as possible models.

Beginning with the last species, Hillyard and Vinegar (1972) noted that when pool temperatures were great, thus dissolved oxygen low, individuals of *T. platyurus* would repeatedly come to the surface where O_2 was assumed to be higher "...and appear to ventilate, with their respiratory appendages stirring the surface...." Thus when low O_2 is a problem, behavioral responses appear to keep fairy shrimps in the highest oxygen concentrations available. These same fairy shrimp enthusiasts determined that the metabolic rate of *T. platyurus* varied little with temperature change, particularly at the warmer conditions in which they often swam. Such thermal insensitivity is not at all common amongst organisms, but it does occur, and here we find it used to the advantage of a warm-water fairy shrimp.

More typically, metabolic rate doubles or triples for each 10°C increase. *Branchinecta mackini* is known to fit this scheme. Of course, like the world population, metabolic rate cannot keep doubling. At some temperature it reaches its peak, then declines, and finally the animal dies. For *B. mackini*, its peak metabolic rate is expressed around 8-10°C below its upper lethal temperature of about 32°C (Eriksen & Brown 1980b). Such a wide thermal span above its metabolic maximum suggests this desert anostracan, like some warm-water creatures, can "hang tough", that is, can tolerate the increasingly less favorable conditions as temperatures rise from those which are physiologically optimal. Such a conclusion makes sense because this fairy shrimp is one of the few California species that is occasionally found "doing its thing" in desert flash-flood-formed pools during summer when tolerance is undoubtedly a virtue. However, so as not to lead your thinking and conclusions astray, take note that *Branchinecta mackini* occurs over a temperature range unique among California Anostraca, and, in fact, is most commonly found hatching and swimming in cold and cool waters.

Without scientific studies of strictly cool- or cold-water fairy shrimps to demonstrate how their metabolic rates and tolerance physiologies might work differently, we are left out in the cold (so to speak) for an answer. Coincidentally, *Branchinecta mackini* and its notostracan relative, the tadpole shrimp *Lepidurus lemmoni*, sometimes occupy the same spring pools. If we were to use our research data from this cool-water tadpole shrimp (Eriksen & Brown 1980c) as a suggestive model for how a cool-water fairy shrimp works, we would expect to see little tolerance in the latter of environmental conditions that exceed those at which it demonstrates its maximum metabolic rate. In fact, once that magic temperature is surpassed, metabolic rate would decline catastrophically and the animal would soon die.

But back to survival in warm-water, low-oxygen habitats. As the last solution we can muster, remember that a supplementary method of obtaining and distributing O_2 is available in the form of hemoglobin; that is, hemoglobin binds far more O_2 than could be dissolved in blood without it. Hemoglobin-bound oxygen is picked up from the relatively high O_2 concentration at the body's surface and released in the lower-oxygen environments of tissues. Although hemoglobin has not been documented in all fairy shrimps, Denton has observed red coloration at one time or another in a number of species and, believing its source to be hemoglobin, feels that most species, if not all, can probably synthesize the pigment. If this be the case, then it appears that hemoglobin is made and utilized only over extended periods of tough times as is the situation with *Artemia* (Gilchrist 1954). Keep your checklist handy for recording such occurrences!

Water, salts, and liquid wastes: their regulation

Anostracans live in habitats with amazing extremes of alkalinity and dissolved salts. Combined, these are sometimes referred to as salinity, but we will use the more appropriate term **total dissolved solids** or **TDS**. Just as amazing is the fact that not all that much is known about how fairy shrimps accomplish the feat of dealing with this fantastic spectrum of ionic materials (the dissolved charged particles which in total result in the osmotic concentration of the medium: e.g., Na^+, K^+, Ca^{++}, Cl^-, $CO_3^=$, $SO_4^=$) and the influx or efflux of water that occurs as a result. As a generality, think of the problem this way. All organisms have a certain concentration of various materials in their tissues and blood. If that level strays very much from a given norm, the beast is in big trouble. You are probably quite aware of that for yourself, given all the emphasis your doctor undoubtedly lays at the altar of blood tests.

For an aquatic creature, like our fairy shrimp, water is the medium in which it lives, and that medium moves into or out of its body depending upon whether environment or organism has more water per unit of volume. If water outside is "fresh" and thus contains little dissolved material, water will move into the body where there are relatively more dissolved materials and therefore less water. If this process continues, our aquatic creature soon has a volume problem, and must make its "bladder gladder" by urination. If the surrounding briny medium contains more salts and less water than an equivalent volume of blood, water will move out of the organism, thus dehydrating it. This natural and passive process of water moving from its higher to its lower concentration, into or out of any living thing, is called **osmosis**.

To put all of this into the fairy shrimp's world, imagine the different osmotic consequences of dwelling across the full range of anostracan habitats: arctic-alpine, temperate, and desert pools. The former are typically environments with very little dissolved material of any kind. The fairy shrimp, on the other hand, is relatively loaded with salts, and so water moves into its body, soon presenting it with an excess. At the other extreme, evaporative desert pools often contain higher levels of dissolved chemicals than does the animal, water tends to move out, and dehydration is a danger.

How do anostracans compensate for these ranges of TDS and osmotic water movements? With the aid of the 9 species that have been studied in this way, four of which occur in California, we make the following general remarks. In order to maintain blood at ionic and osmotic concentrations different from that of the environment, that is, to transport substances in a direction opposite to their normal passive movement, fairy shrimps (yea, all animals) must expend energy in a process referred to as **active transport**. *Artemia franciscana*, which resides in California's most briny waters and "...can tolerate a wider salinity range than any other multicellular organism...." (Browne 1993), relies on this process to maintain the concentration of salts in its blood at a level lower, often considerably lower, than that of the environment. Referred to as **hypo-osmotic regulation**, this physiological ability requires several steps, and a relatively impermeable body surface so that the natural tendency of water to move out and salts to move in is considerably decreased (Croghan 1958b). First, *Artemia* drinks its salty milieu. Because the gut must be highly permeable to allow products of digestion to enter the hemolymph, salts from the water that it engulfed also enter. Second, because NaCl in the blood is maintained at an elevated level over that in the gut, active transport must be responsible for the difference. Because tissues generally have not evolved a mechanism "...that can...transport water against large osmotic gradients.", by actively taking up NaCl, the tendency for water to move osmotically from *Artemia*'s tissues to its intestinal fluids is lowered to "...a level that the active mechanisms for water uptake can overcome." (Croghan 1958d). In this way, the animal gains water from a very salty environment that otherwise would passively dehydrate it. Third, and lastly, because the increasing NaCl content of the blood cannot long be tolerated, *Artemia* must actively transport the excess back into its surroundings. It does this not at the gut surface but via specialized salt-secreting cells in the epidermis of the branchiae of the swimming appendages (Croghan 1958c).

Some California fairy shrimps, like *Branchinecta mackini, B. gigas*, and *B. campestris*, are found in pools which vary widely, both geologically and seasonally, in their dissolved salt concentrations. When the environmental TDS is low, individuals of these species maintain body fluids at a more or less constant osmotic level above that of their pools (**hyperosmotic regulation**). Regulation continues until the concentration outside equals the concentration inside (**iso-osmotic** point). As salts in their pool water rise further, the animals then **osmoconform**, that is they "mimic" the TDS of the fluid in which they swim. However, once the dissolved materials in the blood increase to a point that is no longer physiologically tolerable, the animals perish. A greater tolerance of salt in body fluids explains why *B. campestris* can be found in saltier environs than *B. mackini*, as well as why the latter may occur at times in more concentrated solutions than *B. gigas* (Brock 1988). California species have not cornered the market on this mode of physiological adaptation. In the land down-under, Geddes (1973) noted similar adaptations in two Australian species of fairy shrimps .

Finally, there are anostracans that live under the narrow constraints of water nearly as dilute as the rain. For these moderate- to high-altitude species, the problem is to get and keep salts, and to pump out the water that is constantly moving in osmotically. Although none of the California species living in dilute environments have had their water and body-solute regulation studied, several European fairy shrimps dwelling in similar habitats are known to maintain their blood at an osmotic level higher than the medium in their pools, which is to say they are hyperosmotic regulators (e.g., Panikkar 1941; Ralph 1967). These species have adapted differently from those just discussed in that they are able to regulate the concentration of their body fluids in waters of much lower salt concentration ("soft" waters), but die when the environment is saltier than themselves because to osmoconform means death. Horne (1968) believes that because all branchiopods have blood osmotic concentrations much lower than other crustaceans (Potts & Parry 1964), thus a lower osmotic gradient between body and environment, these creatures osmoregulate more easily in freshwater. Assuming this to be true, the ability would contribute significantly to the success of fairy shrimps in very dilute habitats.

In the process of osmoregulation, animals differentially regulate ions. In other words, while one ion in the blood is increased to some level, another may be increased or decreased to a different proportional concentration. Having said that, what do we know about the ion-regulatory ability of anostracans? Little! Six of the 8 species that have been investigated in this way dwell in California. Although ion regulation of K^+, Ca^{++}, Mg^{++}, and Cl^- has been briefly studied, most work has dealt with Na^+. For example, Horne (1968) demonstrated that Na^+ was actively taken into the body of *Eubranchipus bundyi*, even in waters very low in Na^+, and concluded from this that the species was well adapted to dilute habitats. *Branchinecta sandiegonensis* and *Streptocephalus woottoni*, also inhabitants of dilute rain pools, *Branchinecta mackini* which lives in much more concentrated alkaline waters, and *B. lindahli* which dwells in both kinds of places, are described as being regulators of Na^+ over certain environmental ranges. In habitat concentrations above and below their regulatory ranges, these fairy shrimps are Na^+ conformers until they perish (Gonzalez *et al.* 1996). These authors explain the different distributions of the three species by how well they tolerate Na^+ conformity at either end of their regulatory ability. For example, both *B. sandiegonensis* and *S. woottoni* sustain their blood Na^+ levels in the face of quite low habitat concentrations. However, following the cessation of regulation at higher environmental Na^+ concentrations, and as its level in the blood begins to rise along with that of its pool, individuals begin to die; and so these species are restricted to waters of rather low-Na^+. Although *B. mackini* is able to keep blood Na^+ from increasing as rapidly as that of its habitat, the animal is a poor hyperregulator of the ion. Absence of this species in low-Na^+ waters suggests that low levels in the blood are not tolerated; by contrast, comparatively high blood Na^+ is endured as it conforms to elevated environmental concentrations, and so relatively high-Na^+ waters are suitable habitat. Except for minor details, these same trends were mirrored by two Australian *Branchinella* species for Na^+, K^+, and Ca^{++} (Geddes 1973). Continuing with the Gonzalez *et al.* (1996) study, *Branchinecta lindahli* is viewed as a creature which reacts in the same way as *B. sandiegonensis* and *Streptocephalus woottoni* in low-Na^+ environments, and mirrors *B. mackini* throughout the rest of the range tested. You may not be too surprised to learn, then, that *B. lindahli* is found in pools similar to those occupied by the other three species.

When fairy shrimps typical of so-called "soft waters" regulate osmotically and ionically, where do they obtain the needed salts? Remember that brine shrimps spend energy in the process called active transport to **counter** the natural movement of ions from the briny water in which they live to their lower body concentrations. Assuming active transport can function whether the normal osmotic direction be out of, or into, an organism, then such a mechanism, evolutionarily honed for soft-water anostracans, could account for movement of salts from lesser amounts in the pool to greater levels in the animal. Panikkar (1941) thought this to be true for the European fairy shrimp *Chirocephalus diaphanus* and further claimed that branchiae of the phyllopodia were where this was accomplished. Add to the possibility of active uptake of ions the fact that a modicum of minerals is ingested in food, and we have the best guess as to how our soft-water fairy shrimp friends gain and regulate their salts.

When you and I think of kidney function we tend to think of eliminating urine, a solution of mainly water and urea, the latter being a toxic nitrogenous waste produced in the breakdown of proteins. Although fairy shrimps may eliminate a small amount of urea in the water they pump out, about 75% of their nitrogenous waste is ammonia (Bernice 1972). Ammonia is a highly soluble gas and rapidly diffuses away from the animal through the same surfaces by which it takes up oxygen.

Several times we have made mention of fairy shrimps pumping out excess water, yet we have not identified the pumps. Adult anostracans possess **maxillary glands**, so called because their ducts open at the base of these head appendages. Such glands are remnants of excretory organs, analogous to kidneys, used by ancestors of crustaceans. Apparently they play only a minor role in salt regulation of present-day fairy shrimps; however, the best guess is that they still function as bilge pumps by dumping excess osmotically-derived water (Croghan 1958d).

Reproduction

Those people who are gently touched by intently observing fairy shrimp mating behavior generally subdivide the process into a series of actions (Belk 1991a) which could probably define their own. Such beautiful steps, so coldly enumerated, are: detection, orientation, station-taking, clasping, copulation, ejaculation, and disengagement (sigh!). Perhaps before discussing the intimate details of these activities, we must admit that there have not been all that many scientists who have studied such behavior. In fact, the generalizations of what goes on in the sex life of fairy shrimps come from only 10 of the more than 260 species described world-wide (Belk & Brtek 1995). However, Belk (1991a) believes these generalizations are reasonable "...given the morphological similarity of reproductive structures in the Anostraca...."

Observers have noted that males seem always on the prowl for mates, and while they have demonstrated detection of females by males involves vision, nothing has been established concerning the role of chemicals or water-borne vibrations as cues to males about possible mates. Were we analyzing humans, a male who had detected a female might next be seen to "make a pass" at his prospect. By contrast, fairy shrimps are sorta dull. Orientation merely involves swimming over to the vicinity of any promising object; but with station-taking the activity becomes more intimate. The male of most species moves in below the female (remember, fairy shrimps swim on their backs) and positions his head next to the dorsal surface of her genital segments. Just to demonstrate not all fairy shrimps practice the same routine, males of *Streptocephalus* and *Thamnocephalus* will place their heads just above the female's ventral brood pouch. However, from either position the result is the same. The male aligns his body with hers and follows her every scintillating move.

Satisfied that this lovely creature is for him, the male quickly grabs the female from behind with his antennae by placing them around her body between her last pair of legs and the anterior end of her brood pouch. In typical female fashion, this lady fairy shrimp not uncommonly resists the male's embrace by briskly thrashing about, an activity which often results in her escape. This certainly illustrates that throughout the animal kingdom, including humans, not all males are acceptable to every female at any moment, and that females are involved in choosing a male rather than merely being overwhelmed by any one that happens by and demonstrates active interest. Although not all the cues used by fairy shrimps in choosing mates are known, evidence suggests species-specific antennal shape and ornamentation do aid the female in choice of a male (Belk 1984).

Once the procedures for evaluating a prospective mate are complete, and the male in question is found acceptable, clasping occurs, an activity which may last only a few seconds in streptocephalids, thamnocephalids, and the branchinectid *B. lindahli*; several minutes in *Eubranchipus serratus*; a few hours for *Linderiella occidentalis*; or days as seems to be the case in *Artemia franciscana* (whew!).

During these swimming soirées, with the male in firm clasp of the female, he curves his body around her abdomen then attempts to insert one of his penes through her genital pore and into her ovisac. She will generally not allow his entrance if already carrying fertilized eggs. However, when ripe eggs are present several struggling efforts may precede ultimate success. Not surprisingly, successful copulation, which lasts from only a few seconds to several minutes, is very stimulating to the male, and he soon ejaculates. For those so inclined, sperm can be watched flowing into the female's ovisac in slow-mating fairy shrimps like those of the genus *Eubranchipus*. Watched or not, once the ejaculatory act is finished there seems to be no biological sense for hanging around, and the pair soon disengages. In the inseminated female, "shutters", which separate the ovisac from the lateral pouches where eggs have been stored, now open, allowing eggs to flood into the ovisac, mix with the sperm, and be fertilized (Criel 1980). The male, as males are sometimes prone to do, swims off to detect another female whose delicately beating phyllopodia and enticingly protruding brood pouch lure him to repeat the sex-behavior sequence. Ah, those insatiable males.

If one were to try to draw meaning from variation seen in the reproductive process just described, unsurprisingly, ecological realities are probably at its root. For example, fairy shrimps typical of hot, short-lived, fast-drying pools might be described as of the "wham, bam, thank you ma'am" type. In pool's with an intermediate longevity, fairy shrimps are more deliberate as they proceed through the reproductive process. Finally, long-lived waters sport species which stay in each other's embrace for an extended period of time; and why not, there is no need for hurry.

Development of cysts

Immediately after fertilization not only does embryonic development begin, but the shell glands of the female secrete chemical substances into the mix of seminal fluid and fertilized eggs. Then an amazing thing happens. This material forms a thick, usually multilayered shell around each developing embryo. Talk about "better living through chemistry"! By the way, this layering is not at all analogous to dipping fish sticks in batter then congealing it in place by frying. Instead, as the material solidifies different layers develop, some spongy, some solid (De Walsche *et al.* 1991; Lee *et al.* 1994); and of course the elaborate structural details developed in the various species also vary wonderfully. What controls formation of architecturally different layers, the variation within species, and the intricate differences among species, lies in the realm of the unknown.

Adaptive significance of structural differences among shell layers has been the subject of some conjecture. Structure is not just for structure's sake, so the suggestions are based on the universal relationship between the way something is built and its function. With regard to the spongy layer, its interstices are of course filled with fluid when formed in the ovisac; but when the cyst is deposited and dries, the moisture is replaced by air. The suggestion has been made that these spaces, like those in a down vest, offer thermal insulation to the cyst. Frankly, we find this supposed benefit difficult to imagine given the tiny size of cysts (0.15-0.40 mm) and the long periods of time they must withstand high or cold temperatures or both. A much better suggestion it seems to us is that trapped air makes cysts buoyant when water returns, a condition which helps elevate them from the sediment and allows them to float. Floating not only makes them subject to passive dispersal within the pool (De Walsche *et al.* 1991), but also places them in higher O_2 concentrations necessary for the energetic hatching process. If the cyst walls of fairy shrimps function as do those of clam shrimps, and there is no reason to believe they do not, then they also provide some physical protection from abrading effects of soil particles being moved by water or wind, as well as from lethal effects of ultra-violet light (Belk 1970).

Although we have commented on the amazing cross-sectional structuring of the wall of the cyst, we would be remiss not to inform you that its surface-sculpturing is just as amazing, and varied, and often species specific! (See Fig. 3.2, p. 56). Richard Hill of the Environmental Office of CalTrans in Sacramento and Bill Shepard of Cal State University, Sacramento, are working on a scanning electron microscope (SEM) photographic catalog for cysts of all California species. Watch for this one! But in the meantime, refer to work by Mura (1991a, 1992b) where you can see most of the cysts of *Branchinecta* species from North America, and California's *Thamnocephalus* and several of its streptocephalids. The publications of Brendonck and Coomans (1994 a,b), where cysts of *Streptocephalus* species of Africa are displayed, give you a good idea of the variety exhibited in this genus.

Concurrent with shell development, embryonic development, which also began immediately after fertilization, proceeds apace for a day or two. During the process the embryo molts (sheds its exoskeleton) once or twice, adding the shed membrane(s), the last of which is called the hatching membrane, to the inelastic and protective shell, or tertiary envelope, surrounding it (Belk 1987). When development reaches a late gastrula stage, further maturation stops, metabolism is drastically slowed, and the embryo is isolated from the environment by a membranous barrier through which only gases and water freely pass (Drinkwater & Clegg 1991). So, the **cyst**, or "resting egg", is really a shelled embryo, analogous to the seed of a flowering plant, in a state of suspended development referred to as **diapause**.

At this point the cysts of most species are ejected through the genital pore to fall to the pool bottom, or, like the Titanic, the female carries them to the bottom enmasse at the time of her death. In some cold-water species, however, development takes a relatively long time with the result that some of the process occurs after the cyst is dropped into the pool (Mossin 1986). If the female survives for an extended period, she will continue to move successive clutches of eggs into her ovisac, each clutch being fertilized by a new mating, most likely with a new male. However, each batch of eggs undergoes development and ejection before the next clutch can be similarly processed. In long-lived species like *Streptocephalus sealii*, Anderson (1984) estimated that a single female, living for three months, may produce more than 1,500 cysts. Wow!

Both the Mono Lake and San Francisco brine shrimps may alter the typical reproductive pattern just described. Their fertilized eggs can remain unshelled and continue development in the ovisac until a larval stage is reached. Swimming young are thus expelled rather than cysts. For those who like to add to their vocabulary, the latter reproductive process is said to be **ovoviviparous**, while those with the more typical pattern are referred to as **oviparous**. Females of *Artemia* switch between the two depending on environmental conditions. And what are the environmental cues? Perhaps a favorable growing season, as indicated by sufficient oxygen, and water at an appropriate temperature and salinity, stimulates larval release, whereas more stringent environmental conditions trigger cyst development.

In large, comparatively static systems (e.g., Mono Lake), cyst production may be triggered when the length of day becomes too short, while in temporary waters high salinity, low O_2, and extremes of temperature are more likely the triggering factors. There is even evidence that individual females of *Artemia* differ in their genetic tendency to reproduce more commonly one way or the other (Lenz 1987; Lenz & Browne 1991).

When mature, cysts, like plant seeds, can withstand extreme environmental conditions. Because of their protective coatings built of materials not affected by the enzymes pepsin, trypsin, or lipase (Horne 1966), they are not digested when moved down the intestines of animals as long as they have not been punctured or smashed in the process. But it is when desiccated, and cysts are nearly free of moisture, that tolerance of real extremes begins (Clegg 1967). For example, they can now be subjected to temperatures near boiling (Carlisle 1968), be frozen for months, even withstand near vacuum conditions for 10 years without damage to the embryo (Clegg 1967). Of course these are the abilities which allow anostracan species to be distributed through alien environments and over great distances, as well as be adapted to a life in basins which dry or freeze solid sometime over the course of a year. And also as with plant seeds, cysts do not hatch until they receive **proper** environmental signals suggesting appropriate conditions for the species to successfully complete its life cycle.

In mountain snow-melt pools, the appropriate stimulus (perhaps cold, pure melt-water) presents itself unfailingly each spring, and cyst longevity need not be great. Having said that, no one knows what a cyst's life expectancy is for species living in predictable waters of this type. In the desert regions of California, one of the necessary stimuli, water, may not come for years on end. During such extended periods, cysts must also ride out temperature extremes that humans might see as verging on the ridiculous. During the summer, soil temperatures reach in excess of 65°C (150°F) day after day. Carlisle (1968) even describes temperatures of 80°C in the desiccated soils of African pool basins containing cysts of *Streptocephalus* and the tadpole shrimp *Triops*. During the course of winter, cysts may be warmed daily, but frozen each night. Still, under such conditions at least some of them survive 15 years, while others can probably make it more than 2-4 times that long. We say this with some authority because Clyde has stored dry soil samples from that wonderful Montana "Cow Paddy Puddle #1" (Eriksen 1966), containing cysts of *Streptocephalus sealii*, for 25 years, and had many successful hatches when water was provided. By contrast, Clegg (1967) noted viability of *Artemia* cysts decreased with time to the extent that only a few released larvae after 15 years and none were viable at 28 years. Although it may be folklore, Clyde swears he has read somewhere that a reasonable percentage of *Artemia* cysts hatched when doused with water after sitting in a vial on a museum shelf for about 100 years. Such a remembrance is given credence by the report that exploratory oil drilling near Utah's Great Salt Lake yielded buried *Artemia franciscana* cysts, carbon-dated at about 10,000 years old, a small number of which hatched when placed in water (Browne 1993). True or not, **ain't life amazing – and wonderful?**

Hatching

Cysts are usually dried, frozen, or both before even more cues finally break dormancy and the hatching sequence begins. An exception to this is the Mono Lake brine shrimp. Because Mono Lake is permanent, the opportunity for drying or freezing is small. Therefore, *Artemia monica* has developed a mechanism that makes environmental sense – a long period of fall and winter incubation at low temperature before the return of somewhat warmer water in spring induces hatching (Lenz 1980; Dana 1981).

In other anostracans, the return of water and any number of supplementary environmental stimuli, acting singly or in combo, are possible stimulators of the hatching process. Among them, temperature always exerts a fundamental controlling influence (Belk & Cole 1975). In at least two desert species, we know the rush of low-salinity water onto the dry, saline, playa lake bed where cysts lie dormant triggers hatching (Brown & Carpelan 1971; Daborn 1975), and when dissolved materials increase to around 1,000 ppm, hatching ceases. Brock (1965) claimed that low O_2 is the hatching trigger for *Eubranchipus bundyi*. However, Mossin (1986) convincingly refuted that notion by showing high CO_2 or low pH is actually the stimulus for a related species, and by arguing that sufficient oxygen must be available to allow the energetically expensive hatching process to occur. While hatching takes place only within a limited range of temperature (Belk 1977a), and clearly not the same range for all California species, those of us familiar with fairy shrimps readily admit that the real complex of environmental cues for hatching is unknown for most species.

No matter the state of our knowledge, once the appropriate environmental stimuli present themselves, and only then, does dormancy end and development begin again. Byproducts from this reinitiation of metabolism accumulate around the embryo, so water moves in osmotically and stretches the flexible hatching membrane. The resulting outward pressure breaks the inflexible outer membrane, if present, and the shell. Further expansion ruptures the hatching membrane and, voilà, the embryo is freed to meet the dynamic challenges of its aquatic world (Fig. 2.1, p. 25) (Belk 1972, Rosowski *et al.* 1997).

Mossin's (1986) studies of a species of *Eubranchipus* revealed a variation on the timing of this process that may be widespread among cold-water forms. Here, in late fall or early winter, the embryo falls free of the shell but remains in a quiescent state (referred to as "prehatched") in the small cocoon formed by the hatching membrane. Finally, when ice melts in early spring, additional environmental cues trigger activity, and the larva emerges into the larger volume of its pool.

Given genetic variability among cysts, and the microenvironment each occupies by chance in a pool basin, not all hatch at a given wetting. However, those that release larvae do so within a limited time span – at most a few days. And with the hatch, the cycle of events that leads from desiccated, embryonated cysts, through tiny larval stages, to gracefully swimming adults is repeated once again as it has since the early morning of crustacean time.

When hatching happens, out pops a one-eyed, egg-shaped young larval stage bearing three pairs of appendages called the **nauplius** (Fig. 2.2, p. 26). In some species a **metanauplius** appears, this being a slightly more developed stage in which the beginnings of thoracic phyllopods are visible (Fig. 2.2, p. 26). Both types of larvae swim jerkily using their three pairs of functional limbs. Although you certainly would not guess it at this early stage, these appendages are really the fairy shrimp's two pairs of antennae and its mandibles. Because growth is limited by the exoskeleton, the latter must be unzipped and cast off, that is, **molted**, for increase in size to occur. And so it is that at each molt these amazing creatures will enlarge in length and girth as they add segments with their attendant appendages. The process continues from nauplius, through metanauplius and juvenile, and into adulthood. Such gradual, incremental growth contrasts starkly with the metamorphic growth of butterflies whose form changes drastically as they pass from egg to larva to pupa then adult.

We don't think further elaboration of anostracan embryology is pertinent to our book, so we've

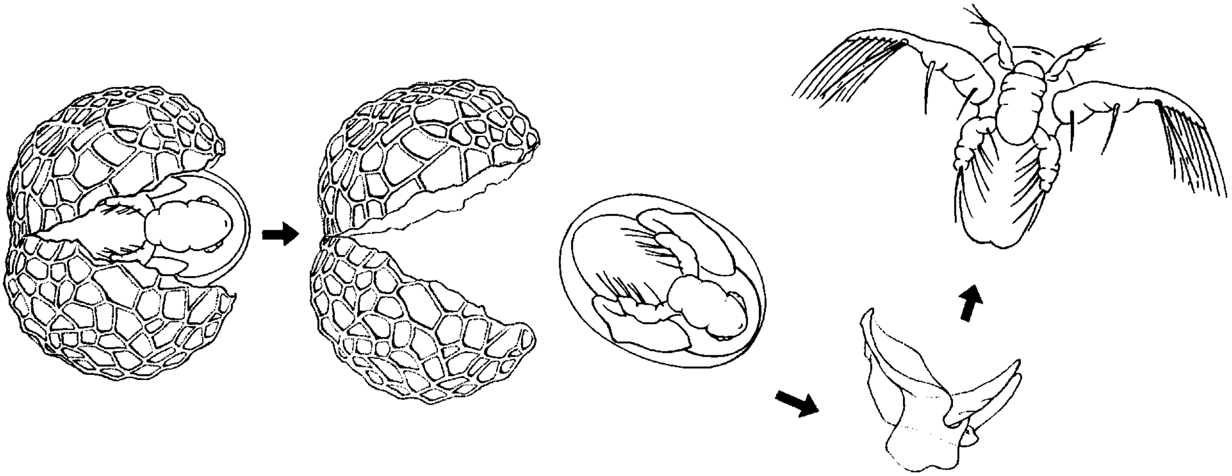

Fig. 2.1. Sequence of events in the hatching of a fairy-shrimp cyst.

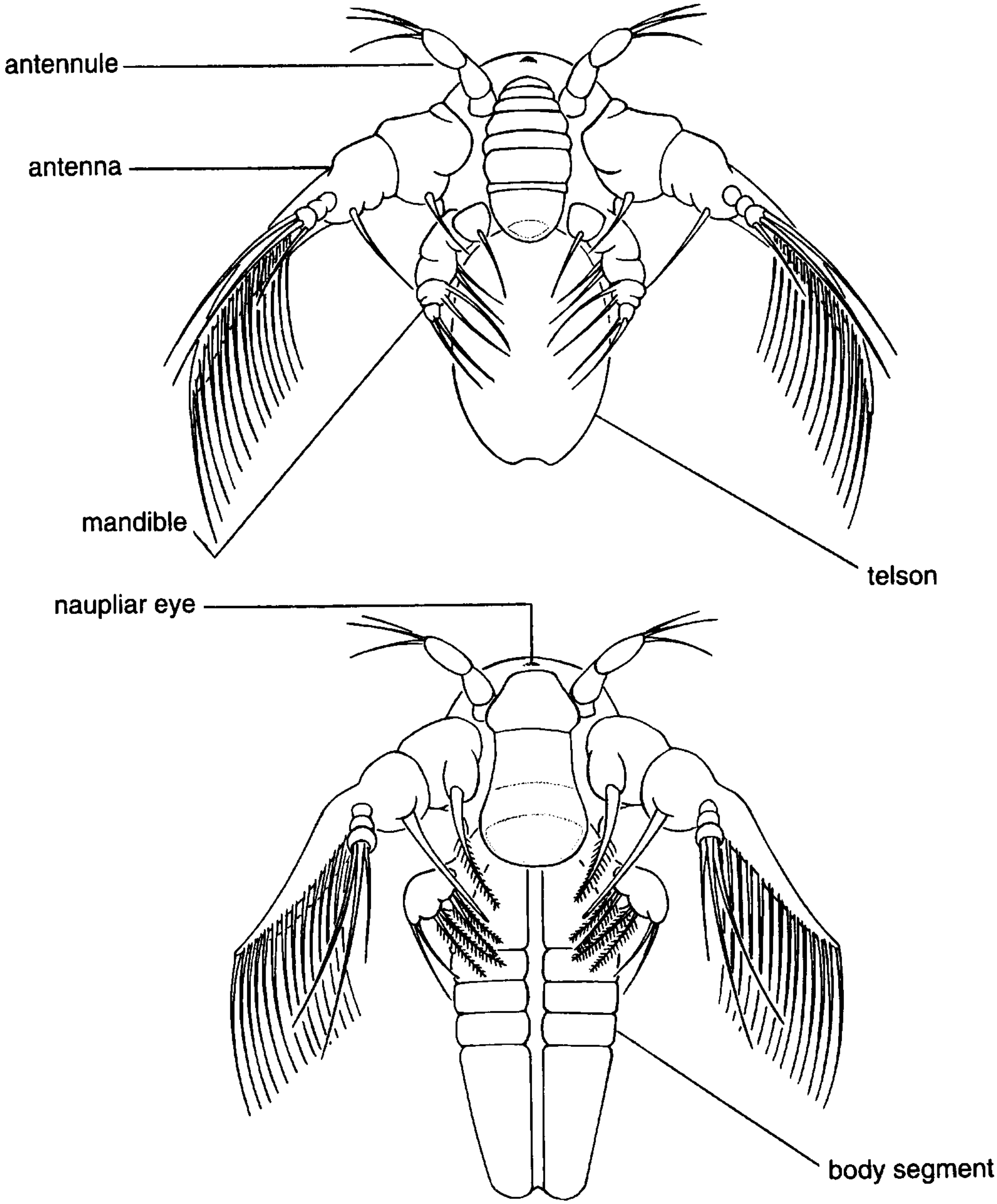

Fig. 2.2. Larval stages of fairy shrimps: Nauplius larva (above) and metanauplius larva (below).

neglected it entirely. However, should developmental details "tickle your fancy", the studies by Weisz (1946, 1947) of *Artemia*, and that of Fryer (1983) using *Branchinecta ferox*, will supply enough material, both external and internal, to satisfy most any appetite.

We encourage you to reserve for yourself some quiet time for inquiry over a minimum of three weeks, and watch the anostracan population in a near-by rain pool. You will not only be richly rewarded by seeing these changes occur before your very eyes, but you will be able to place these events in the real-life drama that is daily unfolding in the microcosm of your special pool.

Unfortunately for some of you, a rain-pool may be inconveniently far removed from your urban setting. Others may get the urge to observe and share these marvels of life with their kids at an ecologically inappropriate time of year (no rain). Some may be barred from a pool because it harbors endangered species (see Chapter 6). Not to worry, merely visit your local aquarium shop and there you can inexpensively, yea cheaply, purchase "sea monkey eggs" (*Artemia* cysts) or adults. Should it be the cysts you bought, merely follow some simple steps on the package, and watch the amazing developmental and reproductive processes anywhere at any time.

Color

Fairy shrimps are graceful and gorgeous, but conspicuously colored? Only sometimes. Most are semi-transparent and a nondescript gray-white. Of the variety of hues that may beautify these animals, the sources of many are unidentified, and the environmental cues that stimulate their production are largely enigmatic. But don't let that interfere with your sharing our delight in the startling range of colors exhibited one spring day by *Branchinecta lindahli* at Emerson Dry Lake, a playa in the western Mojave Desert once used by Marines for gunnery practice. In a bulldozed ditch filled with muddy water, my colleague John Moeur and I (Clyde) spotted brownish fairy shrimps. Such a color is not uncommon in turbid waters, but it is **not** because the animals are dirty, nor is it due to the clay particles which fill their guts; what the environmental cause and physiological source may be are unknown. In a bomb crater nearby, the fairy shrimps, though beige in this water of lesser turbidity, possessed a reddish cast. Dipping into the next turbid-water crater, our net yielded reddish males and pinkish females, probably a result of different amounts of hemoglobin in their blood. This was an interesting find because we had never seen *B. lindahli* with hemoglobin. The last site, another bulldozed trench with turbid water, produced females that appeared dark bluish-green, but this time the pigment was deposited in tissues along the ovaries and in extremities of the appendages. And what about the males? Paint them beige, much like the color of all shrimps from the initial site.

Branchinecta lindahli is widely distributed both within and without California, and is found in a wide range of turbidities and dissolved solids. Its California color variations, which also include red-orange and apple-green, seem to have no obvious connection with these physical factors, for in turbid and clear conditions, high and low TDS, and cold or cool waters, the animals' most common color is the signature milky gray-white of most fairy shrimps. The blue pigmentation we noted might hinge on a diet high in ß-carotene, for such a diet appears to result in blue ovaries in *Artemia* (Hata & Hata 1969) and *Thamnocephalus platyurus* (Maeda-Martinez *et al.* 1995b). We find this scenario unsatisfying, however, because water in all depressions was turbid and therefore must not have been oozing with phytoplankton, all of which possess ß-carotene. Besides, although all water holes had filamentous algae (which also contain the substance) tangled in the branches of brush that ringed the surface water, algal filaments have only occasionally been reported amongst gut contents of fairy shrimps (Maynard 1972; Belk & Ballantyne 1996), and only one pool had individuals decorated with blue ovaries. While reviewing this manuscript, Robert Brown of CSU San Luis Obispo reminded us that *Branchinecta mackini* also possesses a blue pigment in tissues of its oviducts and it too lives only in turbid waters. Whatever its cause, the blue substance may be canthaxanthin-lipovitellin, a material identified from yolk platelets of *Tanymastix stagnalis* (Zagalsky & Gilchrist 1976). Lastly, the cause of blue deposits in appendages remains unknown as well, but it has not been connected with ß-carotene in the diet.

Still on the topic of *Branchinecta*, we recently heard from Marilyn Myers, a graduate student at U. C. Berkeley, who netted *B. dissimilis* from a pool in the White Mountains, the highest known fairy shrimp site in North America (3,587 m). This unique anostracan, at this unique elevation, certainly possessed unique brood pouches because they "appeared phosphorescent to me, like they had light glands", Marilyn wrote. Talk about a "White Mountain high"!

Streptocephalus sealii is the most widely distributed anostracan in North America. In most habitats it displays the "typical" gray-white color of fairy shrimps with the addition that its cercopods are orange-red, a color attributed to trans-canthaxanthin (Murugan *et al.* 1995). Walter Moore (1955), the Louisiana scientist who has studied *S. sealii* more than anyone, transferred a dozen of his favorite beasts from a ditch habitat to a forest pool unoccupied by fairy shrimps. The pool soon dried and remained desiccated for over 6 months. When water returned, so did Walter. Yes, he found fairy shrimps, but rather than being gray-white like those he introduced, they were "...dark brown in color, tinged with deep green – typical coloration for forest pool shrimps." Environment certainly seems implicated, but what habitat clue or clues caused the change in coloration of the next generation was not pursued.

Like Walter Moore, both of your authors have reveled in the various colors of *Streptocephalus sealii*. For example, in a Tennessee pool Clyde described it as opalescent, while in a muddy cattle watering-hole in Montana the animals were the same light-brown color as the fluid in which they swam even though the source of the water was a clear, grass-lined "reservoir" in which all individuals were apple-green. In California, *S. sealii* is restricted to the high Sierra and Siskyou Mountains and thus usually to clear, although sometimes tea-colored, water. Animals in these populations are mostly a beautiful deep green-blue, but, in Lassen National Park, Clyde collected light purple individuals in one pool and green ones in another. In these cases the pigments appeared to be dissolved in blood and, to the esthetic detriment of all who would wish to view them, disappeared upon preservation. What the pigments were we do not know. However, Peeters, *et al.* (1994) described a blue substance (artemocyanin) in solution in the hemolymph of both *Artemia* (where it was first described by Krissansen *et al.* 1984) and *Streptocephalus proboscideus*. You might find it interesting that this blue pigment is a break-down product of hemoglobin. But if artemocyanin is truly the substance causing California-dwelling *S. sealii* to be green-blue, then we wonder why there should be a need to synthesize hemoglobin in the normally high O_2 levels of the cool pools in which they occur? We also wonder why no one has reported at least some red individuals, or possibly some strange-colored critters whose hemoglobin is mixed with the green-blue of artemocyanin?

Another *Streptocephalus*, the Riverside fairy shrimp *S. woottoni*, deposits an orange pigment in its cercopods and sometimes along the edges of its swimming appendages. Such a color pattern sounds suspiciously like that in *Thamnocephalus platyurus* placed on a yeast and ß-carotene diet (Maeda-Martinez *et al.* 1995b). In a control, animals given only yeast (no carotenes) were gray-white throughout. The authors suggested that since orange extremities are typical of most *T. platyurus* collected in natural pools, the color is "probably" due to algae in their diet. Sounds simple, eat algae, turn your appendages orange. However, such an explanation skirts the issue of whether algae can grow in the muddy waters typical of most habitats of *T. platyurus* and *S. woottoni*. In several pools near San Diego, not only the extremities, but the entire body of many females of *Streptocephalus woottoni* appeared bright red-orange. All males were gray-white with orange cercopods. The red-orange hue did not remind us of hemoglobin, but if it wasn't this material, or linked to dietary ß-carotene (which we would expect to affect males similarly), then we have no idea of its cause. If it was due to hemoglobin, it might be because females remain in deeper, more oxygen-poor regions of a pool, a characteristic behavior of females brooding fertilized eggs (Belk 1991a), while males spend more time in near-surface waters.

The fact that low O_2 stimulates production of hemoglobin, at least in some anostracans, is best demonstrated in brine shrimps. From the work of Barbara Gilchrist (1954), we know that in salinities less than about 3.5 times sea water (about 125,000 ppm), hemoglobin generally cannot be detected in the animals. However, at concentrations above that amount, animals become increasingly red. Remember, the greater the salinity of water the less O_2 it can hold. Therefore, *Artemia* increases production of hemoglobin, females more than males, as environmental oxygen declines, and by so doing transports more O_2 to the tissues than would be possible in its absence.

Thinking we "know it all" concerning red coloration may get us into trouble, however. For example, several scientists, studying *Artemia* ecology in salterns (ponds where sea water is evaporated to concentrate salts) along their Spanish coastline, noticed that only certain individuals were "a red color". So what, you ask? Why didn't they merely assume it was hemoglobin and go about their research? We suspect they reasoned as follows. If a low-O_2 environment makes the synthesis of hemoglobin advantageous, essentially all animals would possess the pigment, yet only **some** were pink or red. As it turned out, all pink individuals were parasitized by the cyst stage of a tapeworm. One finding deserves another, right? So analyses of body chemistry showed higher than normal lipids, probably related "...to carotenoid pigments conveying a red color...." (Amat *et al.* 1991). You might ask what the relationship is between being parasitized, body color, and lipid content? A reasonable hypothesis is that parasitization leads to castration of the shrimp, and thus loss of its reproductive hormones. A change in hormonal balance affects body chemistry widely, and probably causes the increases in lipids and carotenoids noted. Castration seems not to affect health of the shrimp otherwise; it merely allows energy normally directed into egg and sperm production to be utilized in development of the parasite(s). Red coloration makes the animal conspicuous and thus probably more susceptible to predation by birds – an advantage to the completion of the parasite's life cycle.

Robert Brown tells us of a similar situation he noted with *Branchinecta lindahli* from the Soda Lake area of San Luis Obispo County. In his case, when an unknown parasite filled the body cavity with its cells, the fairy shrimp became white, making infected individuals quite conspicuous. Bob also theorizes that birds feeding in the pools select these animals because they are easily seen – again a boon to the parasites.

Finally, *Linderiella occidentalis*, a small fairy shrimp typical of a number of California's grassland pools, though light gray-white in body color, has red eyes, a sharp contrast to the dark black eyes of all other Anostraca. In nature, most arthropods utilize black pigments to keep light from leaking between units of the compound eye, but why native populations of *L. occidentalis* swim in the face of this physiological generalization is not understood. Sarane Bowen and her compatriots at CSU San Francisco have been able to gaze into the red, garnet, and white eyes of mutants (produced by radiation treatments) of the normally black-eyed *Artemia franciscana* (Bowen *et al.* 1966). She and her co-workers determined that the various pigments were merely different chemical states of a substance called ommochrome (Kiykomoto *et al.* 1969).

You have undoubtedly noted that so far we have spoken only about adult fairy shrimps. Working our way backwards in the life cycle, we know of only three species in which larval color has been recorded for posterity. Dexter and Ferguson (1943) reported brilliant salmon-colored metanauplii of *Eubranchipus serratus*. Gilchrist (1954) noted that the bright red color of newly hatched *Artemia* nauplii is due to carotenoids in their fat stores and not to hemoglobin. As those stores are used over a period of a few days, the color gradually disappears. Lastly, Maeda-Martinez *et al.* (1995b) commented that nauplii of *Thamnocephalus platyurus* are "green-bluish". Denton (previously unpublished) observed that even embryos possess an array of colors. When he deshelled cysts to measure their contained embryos, to his pleasure he found gold embryos in cysts of *E. serratus*; rust, white, and purple ones inside those of *Streptocephalus mackini*; and cysts containing blue-green embryos of *T. platyurus* and *T. mexicanus*. We know of no definitive information about the source of these colors. Ah, embryonic Technicolor, but why?

Obviously many of the reasons for color variation in fairy shrimps are largely enigmatic. But, might this stimulate some of you to seek answers to the myriad of mysteries associated with color? For starters, how about determining the chemical nature of the pigments displayed? When that is done, perhaps other fascinated followers of fairy shrimps will ferret out the factors which signal an animal to mix its cauldron of bodily chemicals in such a way that colors appear which benefit the beast's survival in its ever-changing ecological world. In the meantime, many fans of fairy shrimps, including your authors, will merely remain in awe of some of the absolutely gorgeous colors carried about in the bodies of these gracefully-swimming creatures.

Chapter 3

ECOLOGY OF FAIRY SHRIMPS

Introduction to community ecology

As your mind's eye sweeps across the California landscape it "sees" the great variety of human communities through which you have traveled: from Alturas to Zzyzx, Red Bluff to Redondo Beach, and including Laytonville and Los Angeles. Ah, yes, how they vary: you remember their vast differences in land area covered, in human numbers, cultural diversity, complexity of economy, and esthetics. Some were nestled peacefully amidst the pines along a little-traveled mountain road; others lay pastorally on the rolling grasslands buffeted by winds and threatened only by afternoon thunderheads. Some were but an eyesore along a desert highway; unfortunately, too many were sandwiched and all but choked to death by urban sprawl and the ugly litter of excessive waste. And so it is with the communities in which fairy shrimps dwell, for many are the parallels should one want to pursue such anthropological-anostracan comparisons.

As with humans in their cities, fairy shrimps are often the most numerous "large" and, therefore, conspicuous animal inhabitants of their communities. "Most numerous" usually means these creatures occupy the **first consumer level** in **food chains**. Prudence suggests we explain these bits of jargon involving community economics. In fairy shrimp communities, just as in your own, there are a number of jobs or "functional roles" that when filled provide the "services" that allow the community to function. You may not interact with all your neighbors, but ultimately you and others depend on what they accomplish. For example, you may not know the trash collectors or the bankers, but you would be in a terrible fix were they to take their services elsewhere.

The Great Law for the universe and its living things (Second Law of Thermodynamics), the law that describes the constraints for everything, even the California Legislature, states that ultimately "there is no free lunch", that is to say everything costs something; for humans that might be paraphrased by saying that "using money, costs money". But for a more precise meaning, one which includes planets, people, plant life, pools, ...and fairy shrimps, it is better stated that "using energy costs energy". In other words, all things require and use energy. Because that energy cannot be obtained or used with 100% efficiency, living things are in an insidious, downward, and competitive spiral for the remainder.

Fortunately, one form of energy can be converted to another, like solar energy into food by plants or into electricity by humans, but, in accordance with the Second Law, when conversions occur some of the energy is changed to heat, and heat as we all know dissipates away from our bodies, our homes, and our cars, never to be recaptured. So, the nitty-gritty reality is that as our original energy supply is utilized, some is frittered away, and obviously new supplies need to be sought to replace both use and loss. The latter is a major cost of "doing business", a major controller of the human economy. And so it is with the rest of our universe, including our planet and its other living things, including the economy of the communities in which fairy shrimps dwell.

Fortunately, for humans and anostracans, the sun is a continual source of light energy that can be transformed to a type of energy useful to living things. Although it might strike at the ego of some engineers, conversion of solar energy was mastered more than a few years before their time by certain bacteria, then by lowly algae, and finally by land plants. By the process called **photosynthesis**, plants take the ecosystem's initial step in converting solar energy into the chemical energy of glucose; thus, they are referred to as **primary producers**. Plants then reconfigure glucose into various products to make their own structure (e.g., leaves and wood) and reproductive items (e.g., fruits and seeds). In so doing, plants set the limits for the amount of energy available in a community, for more cannot be used than is produced or imported.

Faced with an inability to convert solar energy to their use, many animals meet their energy needs by eating plants or plant parts which they are adapted to consume and digest. Such plant-eating animals (**herbivores**) are referred to as **secondary producers** or **primary consumers**. These plant-eating animals **use** energy to gain and process their food; therefore, they cannot possibly possess as much energy as they ate, and certainly not as much as is contained in the community's plants. This means that either the herbivore numbers are fewer, or their biological material, as measured by collective weight (biomass) or energy (calories), is less than in the plants.

We also know that the animals we call **carnivores** make a living by eating other animals, not plants. And if our previous argument is followed to its logical conclusion, the carnivores in the community should number fewer, or at least collectively contain less biomass or fewer calories, than the animals on which they fed.

The fact that plants provide all the initial fuel for a community's economy, and that certain animals eat those plants in order to gain their energy, and in like manner other animals eat the animals that ate the plants so that they too may have energy to drive their processes, is of paramount importance to humans, and to fairy shrimps! If you were to gather together all the threads that link the specific feeding requirements of all species in a pool-community, you would weave a particular pattern, yea structure, on the fabric of life that describes your particular fairy shrimp community. The relationships that have evolved among and between living things, in which the energy of some species is captured and processed by others adapted to do so, are what we call **food chains** and **food webs**. In nature, energy flow along these feeding interrelationships is the measure of the community's economy; and success is determined by the efficiency of energy use, **not** by the fantasy of an ever-increasing GNP!

Thus, because of constraints described by The Great Second Law, every creature gracing this earth is obviously concerned with continually "putting food on the table". As it does, it interacts with, or relies on, many creatures that provide other essentials which aid its, and its community's, health and survival.

The fairy shrimp's aquatic community

If we were to visualize the community in which a fairy shrimp lives, one where the ethnic and job diversity is **great**, just who are the participants providing the essential services that we are likely to encounter? Approaching this challenge as an ecologist might, we would first look at creatures who harvest the energy of sunlight. WOW, these come in a fantastic variety of shapes, sizes, and life styles – just as do humans in their communities. No surprise here!

At their simplest, there are the single- or few-celled blue-green bacteria and algae that live a life dispersed in the water column. Biologists call these **phytoplankton**. There are also algae that begin life attached to some stable surface such as the pool's bottom, including rocks and logs, or it may be other plants, living or dead, or even animals! The many creatures which share this way of life are collectively known as **periphyton**, and they are a tasty, nutritious smorgasbord for animals adapted to eat from this table.

Algae are among the most ancient and anatomically simple life-forms on earth; but in the evolutionary scheme of things some ancestors of these aquatic organisms gave rise to more complex terrestrial plants, adapted structurally, physiologically, and reproductively to a life out of water. Inevitably, like many animals (most notably insects), some plants reinvaded their watery origins. The ones who most commonly did so were the flowering plants, members of the community that make most of the "tenement houses" that root in the bottom of a pool and reach for its surface, sometimes piercing it. These flowering plants, from pond-weeds to rushes, create the structural complexity which provides the special habitats needed by many of the pool creatures. These are also the plants that are responsible for the late-season edge-bloom which defines, and colorfully graces, California Vernal Pools.

In their communities, humans watch birds, usually pigeons and house sparrows, circling the atmosphere between the tenements. In a pool, the aquatic "atmosphere" is filled with a much more culturally diverse and therefore pleasing variety of living things. Other than the countless numbers of bacteria and the phytoplankton already described, the midgets on the block include **Protozoa**, or single-celled animals. They teem in great abundance, occupying all levels of the consumer food chain. **Ciliates**, protozoans which possess a great profusion of cell membrane outgrowth which beat to cause rapid movement, are the speedsters of the microscopic world. Also included in this locomotor menagerie are those which have one or several long whips to propel them in spiraling trajectories. These are the **flagellates**. No simple classification of the eating habits of these tiny creatures exists, for many absorb dissolved organic materials while others eat organic particles, and thus are "animals". A number of flagellates possess chlorophyll, and, being plant-like in this way, are included in the phytoplankton as primary producers. Our tidy minds demand simplistic cataloging of community members; real life continually reminds us that to this end we fool ourselves!

Not much larger than protozoans, but many-celled in structure, are the Norelco shavers of the animal world. These microscopic creatures, usually with two rings of beating cilia at their head end that not only propel them through the water but sweep bacterial and algal food to their mouths, are called **rotifers**, or wheel animals. Although fairy shrimps need not concern themselves about collisions with such small-sized traffic, a different story might present itself with other pond creatures. The most common constantly swimming animals other than fairy shrimps are the water fleas (**Cladocera**; Fig. 1.1, p. xiv) and copepods (**Copepoda**). By comparison to adult anostracans, these creatures also are small (usually 1-2 mm). However, by virtue of their sheer numbers, the pool may seem like Times Square on New Year's eve to a fairy shrimp. Where the rub (pardon the pun) arises is most copepods, water fleas, and fairy shrimps are filter-feeders, that is, they filter small particles, including bacteria, protozoa, rotifers, and phytoplankton, from the water through which they swim. Similar feeding habits suggest competition for available "goodies", and so it may be. However, as with the human business world, specialists of all kinds abound which stake out and capture a sufficient piece of the economy. By possessing different-sized filters, or feeding in disparate areas of the pool, filter-feeders can specialize in only certain segments of the total resource and thus either minimize competition or out-compete generalists attempting to benefit from the same resource. Other small and constantly swimming community members include some wonderfully colored flatworms (**Rhabdocoela**), most of which probably use filter- and suction-feeding, and the spidery water mites (**Hydracarina**) adapted for sucking the body fluids of small crustaceans and insects.

Larger members of the community just might include some fascinating close relatives of fairy shrimps spoken about earlier. The clam shrimps, or **Conchostraca** (Fig. 1.1, p. xiv), often lie on the bottom, but as unlikely as it sounds they also spend a good deal of time swimming...and filter-feeding. And, if you are wary of the statement that "truth is stranger than fiction", you might change your mind when you encounter tadpole shrimps (Order **Notostraca**; Fig. 1.1, p. xiv) with rhythmically-beating hemoglobin-filled phyllopodia. These creatures, some upwards of 70 mm long, and feeders on bottom debris and predators on fairy shrimps when occurring together, look like something out of earth's fossil past. In fact, they have changed little from their own fossils, and, given their large, flattened shield and swimming legs, superficially resemble a fossil group of early arthropods, a resemblance that led to a fishery biologist's embarrassing misidentification. When accompanying an L. A. Times reporter to a desert lake to explain what life had burst forth following a rare summer rain, he gasped when he saw tadpole shrimps and exclaimed: "My god, Trilobites! Trilobites haven't been seen on earth for 250 million years". So, go look in **your** pool. Who knows what you will find.

Insects are common in some longer-lived temporary waters and, as you might expect given their fantastic variety in terrestrial habitats, have specialized along a number of aquatic life styles too. You will see snorkelers, aqua-lungers, and gill-breathers, and if such adaptations get the best of your curiosity, check out the chapter on **Respiration** (Eriksen *et al.* 1996) in *Aquatic Insects of North America*. Although many of these insects are small, several of the larger, highly mobile ones are notable predators on fairy shrimps and other pool life. Of these, the predaceous water beetles and their larvae (Family **Dytiscidae**) and a true bug called a backswimmer (Family **Notonectidae**) are the most common. The majority of the other pool insects live on or near a submerged surface, using the latter for resting, protection, and a place from which to launch a feeding foray. Such creatures include dragonfly larvae and their relatives the damselflies (Order **Odonata**), both of which can, and do, chow down on fairy shrimps.

Most of the other creatures which circumnavigate the pool have little direct interest in fairy shrimps. They make a living either by grazing on plants, or by scooping up dead remains enriched by a bacterial and fungal coating – a material you might call "gunk" but which ecologists refer to as **detritus**. Such creatures are called **detritivores** and include mayflies (Order **Ephemeroptera**), caddisflies (Order **Trichoptera**), seed shrimps (Order **Ostracoda**), and scuds or sideswimmers (Order **Amphipoda**). Also undertaking this way of life is a bug called the water boatman (Family **Corixidae**), a beetle called the water scavenger (Family **Hydrophilidae**), and pond snails called "pond snails" (Class **Gastropoda**). As if this menagerie of creatures is not enough with which to rub shoulders or cause traffic congestion, stand back for the "18-wheelers" of the pool. Although tadpoles of most frogs are herbivores, adults are predators, and salamanders and their larvae, long and lanky vertebrates, and also fairy shrimp predators, are big enough to run down and eat almost everything else on the "highways" of the pool.

Fewer, but unfortunate for pool animals, are the voracious wading and diving birds that come and go. Now we can understand the use of the broad and filtering bill of the Northern shoveler (duck) for collecting fairy shrimps. At an earlier and much more naive time of life, your senior author thought the long tubular bill of a wading American avocet was obviously adapted for probing mud flats, not for "filtering" anostracans from a pool's water column! Dare I admit I had a narrow view of the avocet's world? While "doing science" at many a fairy shrimp's home, I have watched in amazement as avocets waved their beaks back and forth in the water and grabbed whatever they hit. What they hit was most likely a fairy shrimp, but was also possibly something which ate a fairy shrimp. Ah, the ingenuity of life, and the beauty and symmetry of a pool's energy flow!

Fortunately for anostracans, circumstance rarely brings them together with fish. The ephemeral nature of fairy shrimp habitat obviously precludes fish in most cases. However, should flooding link permanent and temporary waters, as occasionally it does, and allow fish to enter the grocery store of a pool (e.g., McCarraher 1959; Pereira & Gonzalez 1994), they will find fine cuisine that has no protection but numbers, time, and the forest of pool vegetation in which to "get lost". Obviously this situation is not on-going, for the fish must find their way back to permanent water, or they too will be lost, in this case to the finality of drought for which most of the pool species are adapted, but fish are **not**.

What a complex community it can be! There are the producers (plants), and those animals that make a living eating plants, or eating those that ate plants, or eating those that ate those that ate plants. Finally, there are countless creatures which eat dead stuff – dead plant or animal material, dead of this year or last year, dead of what was produced in this pool or what was dropped or blown into it from afar. **Nothing** goes to waste in nature. Everything is sought and consumed by someone. Here is the true meaning of "**recycling**" which, if the organisms are left to do "their thing", forms raw products that allow production to continue. Here is the dynamic equilibrium of nature in action!

Some pools, like small human resource-based communities, are probably not so grand or complex as just described. Several are the reasons. As physical or chemical conditions become severe and cast a shroud of extremes to which only a few species are adapted, food webs become much simplified. One of the most striking examples is the salty and oftentimes warm waters in which brine shrimps like *Artemia franciscana* and *A. monica* flourish. Bacteria, an algal producer or two, the brine shrimps that filter these kinds of tid-bits from the water, and a detritivorous brine fly may be about the only cast of characters present.

Should you wonder if things can get even simpler, then consider Rabbit Dry Lake, an alkaline playa in the Mojave Desert. Here during dry times we see a hard, flat, expanse of clay shimmering in the summer heat. But when a storm dumps its contents on the encompassing mountains, soil- and organic debris-laden water rushes hellbent to the playa below to fill it with water so muddy it looks like a chocolate milk shake; water so muddy that light does not penetrate and photosynthesis cannot occur. Surprisingly to some, *Branchinecta mackini* hatches and thrives in enormous numbers. Such a prolific event makes it understandable why its major predator, *Branchinecta gigas*, may be present as well, albeit in expected smaller numbers, say one *B. gigas* to

40,000 *B. mackini*. Other than the ubiquitous bacteria, that's the cast of characters, friends! No other visible critters. But, you ask, "if there are so many alkaline fairy shrimps, what serves as their food?" We will provide an answer shortly in the section "What do fairy shrimps eat?"

Most pools, puddles, and playas probably lie somewhere between the extremes described. And should you follow the creatures in your favorite water-filled micro-universe, you will certainly see the comings and goings, searching and eating, reproduction and decay, that all add up to the particular economics of the community. **FASCINATING!**

As intrigued as you may be in your own "personal pool", we ask that you be of broad perspective. Do not get caught up in the simplistic mind-set of some poets, perturbed people, and politicians who believe, at least state, that "if you've seen one, you've seen 'em all", for nothing could be further from reality when dealing with temporary waters. To prove that point to yourself consider reading Balco and Ebert (1984) and Syrdahl (1993). They show, by comparing many features, that each pool is not only different, but usually uniquely so, even from its neighbor. Not only does the cast of actors change through the pool's duration, but the timing of those changes may also be strikingly varied!

Coexistence of species of fairy shrimps

In the previous section, we intentionally said little about different types of anostracans coexisting. Dogma has it that were two or more species to occupy "the same niche" (have exactly the same requirements and do exactly the same thing) they could **not** co-exist. The rationale is that, since by definition they are recognizably different, one of the species must be able to "do its thing" somewhat better, possibly only slightly better; but if so, it would have a competitive advantage, reproduce more, and ultimately predominate to the exclusion of the others. Species which are most likely to compete so intimately are those which are structurally and behaviorally most closely related.

Given such sage words, one might not expect several kinds of fairy shrimps, particularly those within a genus (e.g., *Branchinecta*), to compete equally and thus coexist while occupying what generally appears to be the same niche. **However**, although finding different kinds of fairy shrimps in the same pool is not a rarity, it is atypical, especially in cold-water habitats (Eng *et al.* 1990; Graham 1995; Maeda-Martinez *et al.* 1997). To our knowledge, three species is the record for California, while 6, collected in North Africa by Thiery (1991), is the world mark. So much for dogma! Or is it???

In order to begin our discussion of the intriguing problem of coexistence of species, "Return with us now to those thrilling days of yesteryear when out of..." Laurasia came the thundering phyllopod beats of the great *Eubranchipus* ancestor (Belk 1995), and probably the other ancestral anostracans of most of today's North American fairy shrimps (e.g., *Branchinecta, Linderiella, Streptocephalus*). When it was that founding populations arrived to settle pools in what we now call California is not known. What we do know is that some 10-15 million years ago California's earliest recorded fairy shrimp, a species of *Branchinecta*, plied the waters of an alkaline playa in a savanna or possibly basin-and-range setting near where Barstow (San Bernardino County) sprawls today (Belk & Schram in prep.).

Under similar climatic conditions, whether 15 million years ago or now, even closely-spaced pools often vary considerably as habitats; so, whenever founding populations arrived, natural selection immediately began the relentless process of selecting among different combinations of accumulating genetic variability at each site, thus initiating the continuous procedure of honing each population to its specific conditions.

Whatever the range of conditions was that prevailed around Barstow or throughout the rest of California so long ago, the land forms and climate were not what they are today. The Sierra at that time was perhaps 1,000 m high, and volcanoes spewed their contents across the landscape, particularly over the northern half of the range (Hill 1975). Narrow, shallow seas extended across the Central Coast Mountains in places and into the Central Valley. In what is now southern California, the South Coast Mountain Ranges, although still low, had begun to rise from the hills that preceded them (Oakeshott 1971), undoubtedly creating ever-increasing aridity across the lands to the east.

Now superimpose upon these circumstances considerable change in the geological landscape that began in the neighborhood of 10 million years ago. The Sierra began to rise, and the South Coast Mountain Ranges continued their progressive uplift, blocking further the movement of rain-bearing clouds to the east. Knowing this, we can begin to appreciate the increasing topographical and climatic isolation of pools, as well as California's increasing isolation from much of the rest of North America. Of course the general drying and warming trend since Pleistocene times about 10,000 years ago has further added to the increasing hindrance of gene flow between pools. And so fell the fickle finger of fate that gave us this laboratory called California, which not only offers genetically differing populations of the same species in different pools, but the evolution of a myriad of different species, including its great number of endemic organisms, among which are some of its fairy shrimps.

Isolation of California is not complete, of course, because of several methods for dispersal discussed in the section in Chapter 4 "How fairy shrimps got where they've got". In that context, it seems some species may get around more easily than others (e.g., *Branchinecta mackini, B. lindahli*), given their flexible physiologies and wide distributions, in both North America and California. In Australia, Williams and Busby (1991) note a similar broad occurrence of the tadpole shrimp *Triops australiensis*. But as admitted by these Aussies, and as is true of our two species of *Branchinecta*, no one has looked at their microanatomy with scanning electron microscopy, or protein dissimilarity as evaluated by electrophoresis, to determine if differences among populations exist or are developing. Using such techniques, people are accumulating evidence suggesting that dispersal is not successfully accomplished as often as might be imagined or thought (Belk & Cole 1975; Dumont *et al.* 1991; Fugate 1992).

Still, should chance introductions occur, transplants and residents may be different enough that they utilize separate fractions of the resources in a structurally simple puddle; or they may remain "isolated" from each other by occupying unutilized or under-utilized portions of a large, structurally complex pool (Hamer & Appleton 1991; Thiery 1991). To appreciate the fact that pools can truly be structurally complex, you may have to change your impression that an ephemeral water-body is merely a simple dimple full of water. Although such a view might approach reality in tiny potholes, puddles, and wind-swept turbid playas, deeper, longer-lasting habitats, particularly those containing areas of rooted vegetation, often provide great structural and thermal complexity. Hearken back to our discussion of "The fairy shrimp's aquatic community" (pp. 32-36) for a description of such a place.

With regards to coexistence of species, or lack of same, competition which excludes a species is most likely when the environment is predictable and the competitive advantage is expressed generation after generation. Should habitat conditions change slightly, or considerably, the advantage may be shifted from one type of anostracan to another. Temporary rain-pools and the environments in which they form are normally the quintessential example of habitat capriciousness. Important environmental factors can vary, often significantly, from year to year, and of course through the seasons of any given year (Dexter 1967). These include temperature, time(s) of pool filling, if they fill at all, and how long they hold water. Thus, in absence of a predictable environment that gives a competitive advantage to a particular species, a disturbance-based "dynamic equilibrium" is established between two or more forms, shifting the competitive advantage back and forth, and, as a consequence, allowing coexistence over time. Under these circumstances, competitive displacement (exclusion) occurs infrequently (Huston 1994).

If some level of competition does exist, then what are the structural and behavioral differences that explain its minimization among similar fairy shrimp species, you may ask? Perhaps these filter-feeders have evolved dissimilar filter size, allowing one species to utilize a different size-range of food particles from the total food resource than does another. That animals in different life stages have different sizes of filters, and therefore feed on different foods, seems intuitive. Perhaps different behavioral feeding strategies have come about so that one species feeds more on or near the bottom while another feeds higher in the water column. In other cases, temperatures at which cysts hatch may separate species by season, or if they hatch at the same time, perhaps because of different rates of development, young of one species do not mature until adults of another are on their last leg (or perhaps we should say phyllopodium). As the season progresses, and evaporation of pool water leads to increased salt concentration, one type of fairy shrimp may be stressed and see its population decline while another finds conditions much to its physiological liking and "comes on like gangbusters". In other words, although two anostracan species may be found together occasionally, there should be significant differences buried somewhere in their biology that account for their coexistence. Ah, for inquiring minds to dig in and ferret them out!

So, having explained some of the possibilities for coexistence of species, we must admit there is really nothing important known about the degree of competition among coexisting fairy shrimps. In most biological systems competition is difficult to demonstrate, and no experimental work has been undertaken with anostracans. When coexisting species show differences in structure, behavior, and ecology, we should probably best begin with the assumption that these are expressions of genetic selection which minimize competition between closely related species. However, not much is known about such differences among fairy shrimps. For example, we are aware of only 6 measurements of filter size (Fryer 1983; Mertens *et al.* 1991; Schrehardt 1987; Helm 1998), and four are for species not even found in the U.S., let alone California. What we know about anostracan physiology, tolerances of temperature and salt included, is also fragmentary. Observations concerning behavioral differences are minuscule in number, and reports concerning what life-cycle stages were present with coexisting species are fewer than that.

So much for refined theory, informed guesses, and what we do not know. What **can** we tell you about the coexistence of species of fairy shrimps? Well, we can note which ones have been found together (Table 3.1, p. 45), and we can cite several known examples that may explain how fairy shrimps could coexist in California's ecological settings.

We begin with the association of *Branchinecta gigas* (a predator reaching 150 mm in length) and *B. mackini* (its prey, about 30 mm long). These species obviously share physiological similarities that allow them to live in the same alkaline pools, in the same life stages, at essentially the same time. However, the predator has evolved gargantuan size, the greatest length and bulk by far of any fairy shrimp species, has its adult appendages modified for capture of large prey rather than for filter-feeding, and has evolved the behavioral patterns necessary to catch *B. mackini* for its food. *B. gigas* has also been infrequently recorded coexisting with *B. lindahli*, so its feeding behavior appears satisfactory should the latter be the significant food item in its habitat. Although the main food supply of *B. gigas* certainly consists of anostracans, hors d'oeuvres include various species of copepods which it devours as it swims through the turbid waters of its home (Anderson 1970; Daborn 1975).

Differences in feeding strategy, involving behavior and structure of appendages, have been cited (Modlin 1982) as the reason that two species of *Eubranchipus* coexist in the central and eastern United States. Because so little is known about California's species of *Eubranchipus*, a similar comparison cannot be made here. Yet the general differences in feeding behavior described in Modlin's paper have been recorded for a number of other species, including some in California, so they warrant mention. As we know, fairy shrimps are said to be filter-feeders, but not all are just "pure filter-feeders". Using Modlin's example, although *Eubranchipus holmani* remained in the water column sifting out what living and dead "particles" it encountered, *E. neglectus* (misidentified as *E. vernalis*) added to this repertoire by occasionally scraping the bottom with its phyllopodia and thus collecting a load of detritus. Modlin noted that the tips of appendages of the pure filter-feeder are edged by many fine setae, while the tips of the "scraper's" phyllopodia are armored with spines adapting it for this additional activity.

Also interested in limb structure and feeding differences, Graham Daborn (1979), a Canadian scientist, compared phyllopodia of a number of genera and species. Included among them were three that occur in California, two of which may co-occur (*Branchinecta mackini* and *B. lindahli*) and one of which (*B. lindahli*) has been found at one time or another with 7 other California anostracans. He noted that both *B. mackini* and *B. lindahli*, which attentive eyes have seen scraping at times (Daborn 1977; Tasch 1970; Eriksen, & Belk pers. obs.), also have spines along the outer edges of their appendages. Well, all do except *B. lindahli* females which possess fine setae instead. Could it be that not only are species separated by such behavioral and structural differences, but also that males and females of some species minimize feeding competition in this manner as well? Ah, more questions!

Before we run to the field or lab to look closely at our less-observed species, know that *Branchinecta longiantenna* may be a scraper as well, for some of our old drawings show the outer edges of its appendages adorned with spines (Fig. 3.1, p. 47). If this be the case, then some other mechanism must minimize competition between *B. lindahli* and *B. longiantenna* when they occur together, as in the area around Soda Lake in San Luis Obispo County. By contrast, *Artemia franciscana* is probably a pure filter-feeder, for the outer edges of its appendages possess only long setae (Daborn 1979).

Having just mentioned Soda Lake, let us tell you that this is a very salty place and *Artemia* therefore relishes the place. In late April of 1991, Larry Serpa, a regional manager for The Nature Conservancy, collected not only *A. franciscana* from Soda Lake but, for the first time and still the only time in California, *Branchinecta campestris* as well. Larry did not obtain data on the population structure of these two species, but our best guess is the population of *B. campestris* was declining while that of *A. franciscana* was beginning to boom. We say this because that is what Broch (1969) found in his study of populations of these two species in four lakes in the state of Washington. Broch felt the reasons for his observations were rooted in the different biologies of the species. For example, in Washington, *Branchinecta campestris* begins to hatch early in the season when water temperatures approximate 4°C and salinities are low because of snow-melt and runoff. Although *Artemia* can hatch in distilled water, it needs temperatures in excess of 10°C to stimulate the process. Because *B. campestris* cannot regulate hypo-osmotically, it is limited to the habitat's "low-salinity" phase. By contrast, the hypo-osmotic regulatory ability of *A. franciscana* allows it to live on in the grandiose quantities of salt that accumulate when wind mixes fresher surface water with deeper saltier water, and when evaporation concentrates salts in the later life of the pool.

Physiological separation of stages in the life cycle is also important when *Streptocephalus woottoni*, the endangered Riverside fairy shrimp, co-occurs with *Branchinecta lindahli*. Here is a "togetherness" apparently allowed by differences between the species in duration of development (Hathaway & Simovich 1996). What this all means is that *B. lindahli* hatches well, and in several days, from 5-15° and poorly at 20°C as demonstrated by Denton's work (Belk 1977a), then develops rapidly (1-3 weeks) to maturity. *S. woottoni* readily hatches between 10-20°C, with some larvae even appearing at 25°C, but the process takes 1-2 weeks. Development is slow as well, with maturity requiring 7-8 weeks. Thus, during the cool-water stages of a pool in winter, *B. lindahli* is the conspicuous resident, and it is still holding forth in late February or early March when *S. woottoni* attains sufficient size to be collected in a normal dip net. However, by the time most individuals of the latter species are mature, *B. lindahli* has disappeared, and temperatures no longer drop low enough to stimulate another of its hatches. Why this beast has taken leave when adults can probably tolerate the water temperatures, and almost certainly the water chemistry, is not understood. What we do know about its longevity suggests that age might be the reason. Yep, senile fairy shrimps; and more opportunity for research!

Although the previous story seems straightforward enough, life in the co-occurrence lane isn't necessarily all that simple. Consider that the situation just described occurs in western Riverside County. Yet, but a few miles away on the southern coastal mesas of neighboring San Diego County, the preponderant resident anostracan is *Branchinecta sandiegonensis* (Simovich & Fugate 1992; Fugate 1993). Of the many pools on the southern mesas, in only three deeper ones on the Miramar and Otay mesas have *B. sandiegonensis* and *Streptocephalus woottoni* been recorded together; by contrast, on the coastal mesas in northern San Diego County, where *B. sandiegonensis* is much less common than *B. lindahli*, the former has been collected with *S. woottoni* but twice, the latter a number of times. Furthermore, given that the distributions of the two branchinectids overlap, we find it intriguing that on only three occasions, and only in degraded puddles, have they been found together (Simovich & Fugate 1992; Moeur pers. comm.). We would not argue too heartily with the individual who feels this situation smacks of competitive exclusion, but for the real answer, it's time for some experiments.

By way of introducing you to the secretive escapades of another fairy shrimp endemic to California, we note that collections from the largest habitat of *Streptocephalus woottoni* and *Branchinecta lindahli*, a valley grassland pool in

Riverside County called Skunk Hollow, have never yielded a third anostracan in the flesh. Yet, hatched in the laboratory from cysts in its mud is a third species, *Branchinecta lynchi*. This creature is widely distributed throughout the grasslands of California but is seldom abundant anywhere (also a situation not understood), particularly where it co-occurs with other species. Although no published studies deal with specifics of its life history, Helm (1998) determined that it hatches, like *B. lindahli*, at cool temperatures. Why then has it not been seen swimming in Skunk Hollow? We can only guess. And our guess is that *B. lynchi* was present but, true to form, in such small numbers that it just happened never to be taken in reported collections; or perhaps sampling was not done early enough in the season to record its presence. Coexistence with adult *S. woottoni*, if it occurs at all, must be fleeting, because the latter does not mature until waters warm, usually in spring, by which time *B. lynchi* has probably come and gone. How *B. lynchi* gets on with *B. lindahli* is unknown, but it may be too similar in some way to the better-adapted *B. lindahli* to compete well, yet different enough to "hang in there" in a large, comparatively complex habitat like Skunk Hollow. We suggest this because in situations where pool size is recorded, the smaller and simpler basins housing *B. lindahli* have not yielded *B. lynchi*.

The wide distribution of *Branchinecta lynchi* generally includes the ranges of California's two species of *Linderiella* and that of *B. conservatio*, fairy shrimps which also seem to require deeper and larger pools. *B. lynchi* co-occurs with one or the other of the linderiellas with some frequency, but only twice has it been seen on stage with *B. conservatio*. However, in all situations where these associations were noted, *B. lynchi* was far outnumbered. Why? Maybe pond complexity is involved here too (although no such comparisons have been made); and maybe, at least for the linderiellas, the fact they are different genera means they possess sufficient structural and behavioral differences to allow co-existence. Maybe.

Whatever the case with *Linderiella*, the situation with *Branchinecta conservatio* remains unexplained. So, into the void steps Brent Helm, who informed us recently that he believes he knows why *B. lynchi* cannot tolerate this branchinectid. First, both species hatch when cold water fills their pool basins. Second, *B. conservatio* produces but one cohort of numerous individuals per year, while *B. lynchi* may muster several, each with many fewer individuals. Last, *B. conservatio* is "hyperactive" and consequently sets an amazing swimming and filter-feeding pace. On face value these similarities and differences may seem unimportant for the sparse individuals of *B. lynchi*. And in reality they may not be very important, at least when both species hatch and grow together in winter pools that last 6-7 weeks – a period of time in which each can produce but one clutch of cysts. However, Brent feels that if the two species were plunked together in longer-lived pools (the typical habitat for *B. conservatio*), then, were *B. lynchi* to launch a second cohort, those nauplii would be eaten out of existence by the hyperactive filter-feeding activities of the numerous *B. conservatio*. Great hypothesis, eh?! How about someone stepping up to test it? If someone does, they might begin with the observation that the only time these two species have been observed together was early in 1994 in two pools on the San Luis National Wildlife Refuge Complex in western Merced County. Most of the Refuge pools did not fill until February of that year, and were low or dry by mid-March. This period is long enough for both species to reproduce, but so short as to disallow a second cohort for *B. lynchi*. Perhaps this is a typical period of pool longevity here in the arid western edge of the Central Valley; if so, it might prevent *B. lynchi* from being "eaten out of existence" and thus allow co-occurrence.

Finding *Branchinecta lynchi* with the midvalley fairy shrimp (*Branchinecta* sp.) should not raise eyebrows since both can reproduce rapidly and thus live in short-duration pools. However, because they appear to have similar preferred homes, one might expect *B. lynchi* to have been spotted with our midvalley acquaintance more than the three times so far recorded. Given their close taxonomic relationship, the reason may lie in some form of competition so far unraveled.

Branchinecta lynchi's quite unexpected one-known stand with *B. mackini* occurred in a road-side swale pool where the rather different ranges of these two species happen to meet, at the edge of the Pixley National Wildlife Refuge in Tulare County. Habitat water registered next to the highest alkalinity, and the highest pH and TDS, for any pool known to contain *B. lynchi*, and it was near the low end of these parameters for *B. mackini*. Never being ones to shun hypotheses to explain uncommon events, we suggest such non-optimal conditions for both organisms may give neither a competitive edge and both may struggle in this habitat. Here is another of those myriad of real-world situations that would be fascinating to monitor through the season and over the years in the hope of answering some of our ever-increasing number of questions!

Fascinating stories undoubtedly wait to be told concerning the intertwined lives of fairy shrimps – if only someone would take the time to untangle them! In some cases, particularly in California, it is probably too late, for no one has any idea of what nameless faces were extirpated before we humans even knew who they were. But in the case of two of California's most common and wide-spread anostracans with similar distributions, *Branchinecta mackini* and *B. lindahli*, there are some interesting tales to spin regarding their co-occurrence or lack of same.

Branchinecta mackini, true to its name of alkali fairy shrimp, lives in a wide array of alkaline waters. Strikingly, if one were to consider information recorded from out of state, *B. lindahli*, the versatile fairy shrimp, is in fact more versatile. It is known from an even wider range of alkalinity, beginning in the nearly pure waters of the quartz-monzonite dome pools that Clyde studied at Joshua Tree National Monument, and extending to such a seemingly trying habitat as an "alkali soup" the color of "black ink" in Nebraska (McCarraher 1970). Nothing approaching the latter conditions has been stumbled upon in California.

We read in Gonzalez *et al.* (1996) that *B. lindahli* is a much better ionic regulator than *B. mackini*, at least of Na^+, at low environmental concentrations of Na^+, and as a consequence *B. lindahli* is found in soft waters (low alkalinity, low Na^+) while *B. mackini* is excluded. However, since these authors show Na^+ is treated similarly from moderate to high environmental levels by both species (they conform), apparently different ion-control physiologies are not what separates them throughout much of their range. Fine, you say; but if separation is generally not in the manner that salts are handled, then what, pray tell, does isolate them most of the time?

We begin our answer noting that when *Branchinecta mackini* and *B. lindahli* are found together in our state, their habitats are only moderately alkaline, and are always small, turbid, pools and road-side ditches in the Mojave Desert and southern Central Valley. In fact, when found alone, *B. lindahli* typically inhabits small, sometimes tiny puddles usually low in alkalinity. And given its distribution in the most arid parts of the southern half of California, "small" also translates as short-lived. By contrast, *B. mackini*, if in small bodies of water, occupies those tending to be deeper and therefore longer-lasting, and of greater alkalinity. Perhaps more typical habitats for this creature are playa lakes lying in desert basins.

Some of these playas are very large, and reasonably long-lasting when filled, like the 20 km-long Middle Alkali Lake located in extreme northeastern California, or Rogers Dry Lake, landing site for space shuttles (when dry).

Ah, the numbers of fairy shrimps that must filter their way through such large universes – they cannot but boggle the mind! And in those numbers lies one of the keys to our present story. Of course reproduction is paramount in order to be successful in the game of life, but then offspring must feed, grow, mature, and reproduce again, **all with the resources and within the life span of a specific pool**. If one species competes better and therefore reproduces more, it should ultimately swamp the community with its members and drive its competitor to extinction.

Now consider the reproductive biology of our two critters in question. As you have come to expect, growth rate and length of time to sexual maturity are related to temperature. According to Sharon Maynard (1977), during warm falls *Branchinecta mackini* takes 12-17 days to come to sexual maturity. By contrast, *B. lindahli* requires only 9-13 days. In the cooler temperatures of spring, 21-31 days are needed by the former, while 17-20 are sufficient for the latter. In other words, no matter the temperature, *B. lindahli* matures about 25% faster than *B. mackini*. However, there is a price for early reproduction, and that is one of smaller adult size, with a concomitant smaller clutch size. Of course the more transitory the pool, the fewer are the possible clutches.

It seems, therefore, that *B. lindahli* has a strategy of allocating much energy early in its life to get to maturity in a hurry, with the consequence of small adult size and therefore small clutch size. Because *Branchinecta mackini* spends its energy early on to grow and attain larger bulk, it cannot produce eggs until later. But when it does reproduce, its clutch size is big, often 3-4 times that of *B. lindahli*. In both species, multiple clutches can be assembled in a season – the number depends on the pool's longevity **that particular year**. These different strategies of course favor *B. lindahli* in short-lived pools which may have dried to oblivion by the time *B. mackini* is able to begin producing eggs. And seeing the comparatively greater number of cysts that can be generated by a population of the latter, it is no wonder that it predominates in longer-lasting waters.

Although we do not wish to digress too far from our California species, it seems appropriate to mention that the latter have no monopoly on this strategy. In his central Texas environs, Denton (Belk 1991b) watched *Branchinecta packardi* develop to maturity with both small adult and clutch size in 7 days at Texas summer temperatures, and thus could complete a life cycle in short-lived rock-pools atop the local geological wonder, Enchanted Rock. The slower-developing *Streptocephalus texanus*, common in longer-lived pools at its base, never made it onto the granite dome because by the time maturity was attained (11 days and longer), any moisture up there had been lost to the Texas summer sky. This "Texas two" contrasts with our California cool-water pair by hatching and holding forth under a hot summer sun. These species would have a tough time in California given our inhospitable lack of summer rain! And true to this notion, *S. texanus* has been collected in California only along the furthermost southeast border with Arizona, where Sonoran Desert thunderstorms occasionally fill basins along normally dry washes. And although there seems to be no good reason why *Branchinecta packardi* might not also occur in the same area, so far as we know, it doesn't!

But back to *Branchinecta lindahli* and *B. mackini* and their California homes. Given different development times, it is undoubtedly at the "overlap" of short- and long-lasting pools where the two species are found together. In years of drought *B. lindahli* predominates, perhaps even replaces *B. mackini* if dry conditions continue. In years of plenty the reverse may occur. Should the seasons see-saw back and forth over time, one can understand why both branchinectid species could continue to "hang in there" together in spite of being closely related competitors.

A variation on this theme, which may have its parallel in California although it has yet to be seen, is demonstrated by two anostracan species far away in the south of Europe. At an elevation of 1,600 m in some secluded mountain-pasture pools of Italy, Mura (1991b) concluded that *Tanymastix* and *Chirocephalus*, co-occurring fairy shrimps in her snow-melt study pools, shared the same hatching stimulus, cold water. Yet, one species or the other would dominate or be exclusive in different years. In unwinding the evidence in this thriller, Mura discovered that when the season remained cold, *Tanymastix* developed faster and matured earlier, of course being of smaller size than *Chirocephalus*. Not only that, *Tanymastix* was killed by abrupt thermal increases, a not uncommon occurrence in Mediterranean climates. Its co-inhabitant, *Chirocephalus*, was unaffected by abrupt temperature changes, grew at a faster rate in warmer water, reached larger size, and left a greater number of cysts than *Tanymastix*. So, who comes out "numero uno" in any particular year depends on the day-to-day temperature events in these tiny crustaceans' world.

Because of its wide physiological tolerances, and therefore its wide distribution both in and outside of California, *Branchinecta lindahli* is afforded the chance for many inter-species interactions. Never let it be said that this creature does not take advantage of its opportunities because it holds the record for California (7) as well as elsewhere in North America (7 more). Truly *B. lindahli* is the versatile fairy shrimp.

In the most southeasterly desert in California, the Sonoran, there is a paucity of aquatic biologists searching far and wide for summer fairy shrimps so the data we have are few. In any event, *Streptocephalus texanus* and *Thamnocephalus platyurus* dwell there in the summer heat should thunderstorms dump water on their pool sites. Except that these species are both large, both warm-water creatures; and both intolerant of cold (*S. texanus* being less so), fairy shrimp enthusiasts know little about them, including why, throughout their range, if you find *T. platyurus* you usually find with it *S. texanus* or some other streptocephalid (Maeda-Martinez *et al.* 1997). But, never lacking for a reasonable hypothesis to be tested, your authors guess that the fact these anostracans are in different genera suggests structural and behavioral differences which minimize competition and allow coexistence. Certainly *T. platyurus* is a beast of unique architecture (Figs. 7.1, 7.3, pp. 140, 142), but how its strange form might allow it to cohabit with streptocephalids only the creatures of their pools know at this writing.

In California, the distribution of *Thamnocephalus platyurus* also extends into the Mojave Desert, barely overlapping the range of *Branchinecta mackini*. Although the latter can hatch at summer temperatures, it typically makes its appearance in the cold winter waters more commonly presented within its range. And even though *B. mackini* can live in moderate alkalinity, *Thamnocephalus* is found only in waters of low to moderate alkalinity; so there is a window of opportunity for these species to co-occur, and sure enough they do, in Troy and Bicycle Dry lakes near Barstow in San Bernardino County. For the sake of simplicity, let us once again invoke differences in adaptive strategies and generic structural differences as the most plausible reason at this time for their togetherness.

As a final generalization, predictable, long-lasting pools, which occur in areas of snowfall and consistently greater rainfall in the Sierra and more northern reaches of California, tend **not** to support more than one species of fairy shrimp. The favored reason for explaining this phenomenon is that when pools are predictable and stable, individuals of one species must be better suited than those of another to the yearly-repeated suite of conditions, therefore, in time, the better adapted will outcompete others that have found their way into the pool (Maynard 1977).

Table 3.1. Coexistence of anostracan species in California

species	**found swimming with**
Artemia franciscana	*B. campestris*
Artemia monica	none
Branchinecta campestris	*Artemia franciscana*
Branchinecta coloradensis	*B. mackini*, *E. serratus*
Branchinecta conservatio	*B. lindahli*, *B. lynchi*, *L. occidentalis*
Branchinecta dissimilis	none
Branchinecta gigas	*B. lindahli*, *B. mackini*
Branchinecta lindahli	*B. conservatio*, *B. gigas*, *B. longiantenna*, *B. lynchi*, *B. mackini*, *B. sandiegonensis*, *S. woottoni*
Branchinecta longiantenna	*B. lindahli*, *B. lynchi*
Branchinecta lynchi	*B. conservatio*, *B. lindahli*, *B. longiantenna*, *B. mackini*, “midvalley”, *L. occidentalis*, *L. santarosae*
Branchinecta sp. “midvalley”	*B. lynchi*, *L. occidentalis*
Branchinecta sandiegonensis	*B. lindahli*, *S. woottoni*
Eubranchipus bundyi	none
Eubranchipus oregonus	none
Eubranchipus serratus	*B. coloradensis*
Linderiella occidentalis	*B. conservatio*, *B. lynchi*, “midvalley”
Linderiella santarosae	*B. lynchi*
Streptocephalus dorothae	none
Streptocephalus sealii	none
Streptocephalus texanus	*T. platyurus*
Streptocephalus woottoni	*B. lindahli*, *B. sandiegonensis*
Thamnocephalus platyurus	*S. texanus*
species	**cysts in same basin, but not seen swimming together**
Branchinecta lindahli	*T. platyurus*
Branchinecta lynchi	*S. woottoni*
Branchinecta mackini	*T. platyurus*
Streptocephalus woottoni	*B. lynchi*
Thamnocephalus platyurus	*B. lindahli*, *B. mackini*

What do fairy shrimps eat?

We have said in several contexts that anostracans are basically filter-feeders. They are also described as non-selective particle-feeders. If we put those ideas together, we visualize an animal which indiscriminately removes any kind of particle from the water that its suction currents can bring in and its filter size can retain, be it bacterial, plant, animal, detrital, fine sand, or glass beads offered by some researcher. Digesting its treasures is another story. Because of their undiscriminating eating habits, fairy shrimps are best called **omnivores**, or opportunistic feeders, eating whatever is available. But what are the sizes, or variety of sizes of particles, retained and eaten by different fairy shrimp species? The simple answer is no one knows! The more involved answer which follows deals with what few data exist.

Size of mesh or filter in anostracans has been determined for only 6 species that we know of, and only two are found in California. One, *Linderiella occidentalis*, has the smallest filter recorded – an incredibly tiny 0.3-µm intersetal distance (Helm in prep.). Not much larger is the brine shrimp *Artemia franciscana* with a 0.5-µm mesh, and, with it, life stages from nauplius to adult retain individual bacteria (Schrehardt 1987). That's small food! But being so fine a mesh, it is not difficult to imagine these micro feeding mechanisms clogging if the animals' aquatic world was loaded with particles much larger than 0.3-0.5 µm. Perhaps we have here part of the reason that *L. occidentalis* dwells overwhelmingly in deep, clear-water vernal pools (Helm 1998) where vegetation impedes mixing thus the stirring up of clays, and *Artemia* lives in brines where clays cannot remain suspended because they precipitate if TDS exceeds about 3,000 ppm. Ah, physics!

What tiny or big particles exist in the homes of *Linderiella occidentalis* and are sieved out and eaten is presently being determined by Brent Helm at U.C. Davis. With regards to *Artemia*, the environment offers nothing large, for multicellular life (other than the benthic detritivorous brine fly), cannot live submerged in its salty habitats. Certain single-celled bacteria, blue-green bacteria, and green algae, all very tiny creatures, must therefore suffice for *Artemia*'s nutrition. In order to obtain these cells, a filter with a small enough mesh to sieve out such food was obviously evolved for the job. Ah, adaptation!

Now, what about the other extreme? How large a particle can *Artemia* collect and ingest? Schrehardt (1987) writes that maximum particle size increases from 10 µm for early nauplii, to 30 µm for mid-stage larvae, and 50 µm in adults. Because all life stages filter bacteria, it appears that mesh size does not increase with growth of the animal. Also, it looks as though the ability to consume larger and larger particles as *Artemia* increases in size may be determined by oral dimensions, and the effectiveness of mandibles in reducing larger particles or organisms to pieces that fit into the mouth.

When hollow glass balls of a variety of micro sizes were suspended in an aquarium and filtered by *Streptocephalus proboscideus* (an African anostracan with a mesh size of 3.5 µm), the exact same trend was recorded as for *Artemia*. Here the young engulfed particles from 5 µm (the smallest presented) to 17 µm, while adults managed particles from 5-79 µm (Brendonck 1993).

Well, how about the other Californians? Do we have any ideas about what they can stuff into their mouths? The contents of the guts of *Branchinecta mackini* were extracted by Maynard (1972), and amongst the treasures found were algal cells that ranged from 10-50 µm. Maynard was attempting to compare the diet of *B. mackini* with another branchinectid, *B. paludosa*. She

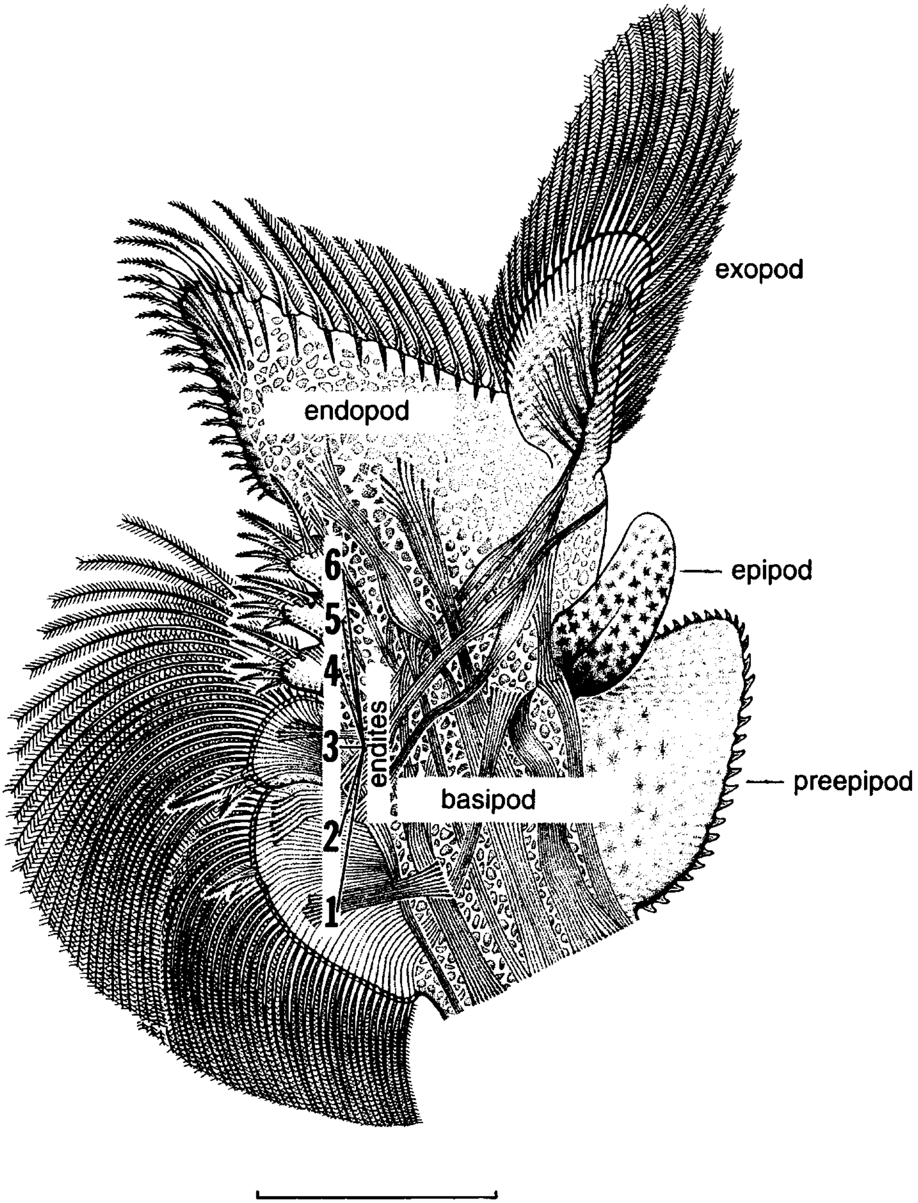

Fig. 3.1. View of the anterior surface of the right fifth phyllopod (leg) of a male *Branchinecta longiantenna*. The numbers 1-6 mark the endites. Endites are inwardly (medially) directed lobes of the unbranched basal part of the leg, the basipod. Scale = 1 mm.

commented that the latter had a coarser, but unmeasured, "filtratory net", a situation which correlated with cells 92-100 µm in size in its gut. Finally, Daborn (1979) counted twice as many setae in the filter area of an appendage from *B. mackini* as compared to one from *B. lindahli*, suggesting a finer mesh-size for the former. Problem! The *B. lindahli* he measured were half the length of the *B. mackini*. So naturally, for these data to be most useful we need to know whether or not setal number and spacing change with an increase in animal size.

How different are the size-ranges of particles filtered and ingested by the various anostracan species? A fascinating study which would begin to answer this question might involve the following. Into one aquarium stocked with similar-sized fairy shrimps of different species, and a second with different-sized individuals of the same species, mix an appropriately wide size-range of glass or plastic beads (industrially available; Brendonck 1993). After the animals stuffed themselves for awhile, ingested beads could be removed from their guts and measured under a microscope. The minimum and maximum diameters, and the size-ranges thus established for each age and species, could then be compared to the measured filter mesh-size of each. Such a study, possibly highly instructive about how the differences in food resources utilized by each species could minimize both inter- and intraspecific competition, has not been done. Will someone step forward to pursue this one? Whoever does, try to incorporate a great idea our editors proposed, color-code the beads for size, for that would make your evaluation so much easier!

Of course fairy shrimps are constant swimmers, so what they filter comes from the water through which they navigate – at least it does for *Artemia* and *Linderiella occidentalis*. Although we do not know how general the situation is, a number of species supplement their feeding by turning over (remember, fairy shrimps swim on their backs) to scrape the flocculent bottom deposits into suspension with their beating phyllopodia. Some return to their normal swimming position with a load of scrapings between their phyllopodia, others swim through the sediment cloud, apparently filtering appropriately-sized particles from it.

So, what are these particles they filter and engulf, and how nutritious are they? In a pool with "clean", clear water the particles are largely phytoplankton and bacteria, but they must include protozoa, rotifers, and tiny larval forms of a variety of species. From present information, we conclude that individual bacteria are probably not captured by the sieves of most species of fairy shrimps because mesh-size is too coarse. Much of the animal material ingested probably gets fully digested. By contrast, phytoplankton cells are surrounded by a cellulose cell wall which is not digestible by animals, but the wall is a rather small fraction of the total cell volume and is permeable to a fairy shrimp's digestive enzymes. Therefore, this array of foods, being mostly digestible, is undoubtedly a very nutritious smorgasbord for anostracans.

In a pool with muddy water, insufficient light penetrates to allow photosynthesis. Particles present may include the animal types already mentioned and bacteria, but phytoplankton is absent. Particles in greatest abundance are the clays that muddy the water. Clay is inorganic and indigestible. So what supports the energy requirements of the fairy shrimps and other community members? The answer is, directly or indirectly, the remaining type of particle, **detritus**.

Detritus is an exceedingly important particle type in pools, be they muddy or clear. It is dead organic matter, largely of plant origin. Its nutritious fraction has already been used by someone or, as with tea leaves, leached into the water as dissolved organics. What remains is composed largely of cellulose and lignin, which are not digestible by macroscopic life. Two questions are immediately obvious. First, if these materials are not digestible by fairy shrimps and others, why are we talking about them? And second, if the pool is turbid and cannot support photosynthesis, where does detrital plant material come from anyway? One question at a time, please!

Although the "large" creatures we visualize as making up the pool community cannot digest cellulose and lignin, bacteria and fungi can. By themselves, detrital fragments are about 5% protein, but after several days in water they are colonized by bacteria and fungi and the protein content of the "combo" rises to about 25% (Cummins *et al.* 1989). To paraphrase Ken Cummins, detrital fragments are like saltine crackers – not much nutrition by themselves, but when spread with peanut butter they become a very wholesome food. So, the organisms that can filter detritus particles from the water and eat them digest the nutritious bacteria and fungi. The still indigestible, but somewhat more fractionated, cellulose and lignin remains are then defecated into the pool where colonization begins anew. Isn't there a well-known saying that goes something like "from detritus to detritus"? Whatever the literary equivalent, detrital cycling is real, and very important!

All that remains now is to get "colonized detritus" into the water in appropriately sized particles and the fairy shrimps can "chow down". Mixing action of wind, and stirring up of the bottom by animal activity, including scraping by some anostracans, are the causative agents. With regard to our second question, detritus which originated outside a pool can be brought to it in several ways. In areas where there is little vegetation to impede movement, wind may blow dead material along the ground, only to have it trapped in a water-filled basin. In grassland areas, overland flow during times of excessive rain or flood, and possibly wind, are undoubtedly important agents of detrital transfer. Where surrounding vegetation is tall, leaves and branches may be blown down into a pool. In the desert, flash floods move not only fantastic quantities of rock particles, but the raging water also picks up leaves, twigs, even bushes that have accumulated in washes, and reduces them to smaller pieces as it grinds its way downhill to the collection basin, often a desert playa, below.

Irrespective of whether a pool is turbid or clear, there is yet another mechanism for transporting detritus. In today's California, cows, horses, and rabbits, probably in that order of abundance, are the main big grazing animals that come to pools to drink. Oh, yes, throw in a few sheep as well. Historically, elk, pronghorn, and deer roamed the California range instead, or go back a step further in time and add mastodons, camels, giant ground sloths, and all other such creatures that are no longer with us. All but the rabbits certainly did not or do not hesitate to wade on in to take a drink. In order to make room for that wet, cooling elixir, these animals are prone to dump their unusable products into their drinking water, yea into the fairy shrimp habitat! Their urine is a fine nitrogen source, and one that can be converted by bacteria to ammonium or nitrate and used by those bacteria, and algae, for growth; the "road apples", "cow-pies", fecal pellets, call them what you may, are fine sources of partially pulverized organic matter. And anyone who has walked through a pasture or along a favorite fishing meadow knows the prodigious amount of processed detritus this source can move (pardon the pun).

There is yet another story that merits telling. Although the process undoubtedly applies to all muddy-water habitats, the details were worked out with *Branchinecta mackini* in a desert playa, Rabbit Dry Lake, by Mike Patten and Louis Rappoport (1980), two students who were working with Clyde. After a steady but non-drenching rain formed shallow pools in the basin without the aid of significant run-off, analyses showed that playa water contained little particulate organic matter. Interestingly, and fortunately, no fairy shrimps hatched into these food-less waters. Shortly after the pools dried, a heavy winter storm created flash floods which brought water, mud, **and organic particles** from the surrounding mountains to fill the playa. Fairy shrimps now hatched and lived happily ever after, well, at least until the particulate organics ran out or the pool dried up. And why didn't the shrimps hatch in the first instance? Was it related to no food? We doubt that one; just how could a cyst determine whether or not food particles were out there? Or, was it the non-drenching rain? Come on now, how do fairy shrimp cysts distinguish between drenching and non-drenching precipitation if both supply puddles, pools, and playas with water?

Back in Chapter 2 we explained that the conditions which stimulate hatching of *Branchinecta mackini* are known, and were also worked out on the Rabbit Dry Lake population. Remember that fresh water, or at least a sudden decrease in dissolved salts, is required to begin coaxing nauplii from cysts. However, when the water's TDS exceeds 1,000 parts salt to a million parts water (1,000 ppm), hatching is inhibited. If we apply this information to the observations of Patten and Rappoport, we realize that the steady light rain which added water drop by drop to the playa's salty soil, plus the constant mixing action of wind on water, assured a high salt content in the pools that formed. The result, of course, was inhibition of hatching. In contrast, when flash floods descend the mountain slopes and fill the playa rapidly, although muddy, the water is large in volume and low in TDS. Hatching is therefore stimulated. Because of the large volume of fluid, several days of wind-mixing of water over playa soils are usually necessary to raise the dissolved salt concentration to a level that inhibits further hatching.

Mizutani (1982), using *Branchinecta longiantenna* (thinking it was *B. mackini*), did some creative lab work to establish what the animal eats. He labeled a common sugar and an amino acid, both of which occur dissolved in playa water, with radioactive tracers. These materials supposedly are leached from detritus brought by flash floods. Physicists tell us that dissolved particles are charged particles, and both of these organic molecules have positively charged ends. Clays, although not dissolved, are so small they too have surface charges, theirs being negative. Ah ha! The clay particles, present in such massive numbers that they make the water muddy, attract and bind dissolved organics, and "hungry" bacteria cluster around and grow on these nutrient-rich surfaces. Such a layering of goodies makes a particle large enough for at least some fairy shrimps to filter, and filter they do, for the radioactive organics were detected in their bodies. Although the clay center of such a concretion is non-digestible, the "peanut butter" on its surface, and dissolved organics held underneath, make for a nutritious morsel. So, fairy shrimps propel themselves through their dark, turbid milieu, seeing little, darting in another direction when they bump into something, but continue filtering nutritious "mud" (or should we also call it a type of detritus?) from the water. Not far down the gut its contents are acidified, and the charged organics are disengaged from the clay. The former, and the bacteria, are digested and absorbed, the clays are moved on and out, ultimately to become suspended particles once more, allowing the process to begin all over again.

You may think we have spent an inordinate amount of time talking about detritus and who eats it, for after all your favorite pool is probably not the color nor the consistency of a chocolate milk shake. For most folks, it is more romantic to think of living things eating living things under clear blue skies and in crystal clear water. However, to put detrital food chains into perspective, consider that probably as much as 95% of an aquatic community's energy flow ultimately passes along such a route; that's only about 5% for the romantics. **Pretty impressive,** or disquieting; depends on how close your esthetic and economic views are to ecological reality!

And speaking of ecological reality, you already know our description of anostracans as being filter-feeders is an over simplification, for many fairy shrimps also scrape detritus from pool bottoms. Further, there are two species which terrorize the crustacean world with carnivory. One, *Branchinecta ferox*, lives in North Africa and Europe and is a filter feeder when small. However, when a length of perhaps 15-20 mm is attained, the animal develops such strong suction currents that it is able to draw in copepods and cladocerans (Fryer 1983). Because this beast grows to lengths of at least 45 mm, it feeds on these animals for a goodly portion of its life.

Branchinecta gigas is the other carnivorous anostracan, and its distribution includes the Mojave and Great Basin Deserts of California. This animal is giant enough that it feeds on other fairy shrimps, particularly *B. mackini*, but *B. lindahli*, as well as cladocerans and copepods, may be significant food items as well. It turns out that *B. gigas* lives only in highly turbid habitats and thus is not a visual predator; in fact, it has by far the smallest eyes in proportion to body size of any fairy shrimp. Because it does not create suction currents that are strong enough to draw in large prey, this fearsome beast swims alertly through its murky medium and reacts immediately upon contact with a potential meal. By drawing its phyllopodia together, the tips of which then overarch the food groove, and at the same time flexing its abdomen over its appendages, our predator attempts to trap its much smaller prey in this "phyllopodial basket" (White *et al.* 1969). If it is successful, the niceties begin with the predator moving the prey forward with the spined bases of its appendages to the mouth area where it is "processed" by the mandibles for ingestion. Armed with sharp denticles, mandibles not only pierce the food when they close, but crush and move it forward as they rotate toward the mouth. Thus Fryer (1966) describes these mandibles not as tearing or chewing devices, but as "crushing rollers". For the trapped fairy shrimp or other crustacean food item, this process is "the end of the line" as the punctured and mashed body is ingested whole. Robert Brown reminded us that although the prey may have been moved into the gut in one piece, it had undoubtedly lost a significant amount of nutritious body fluid. Remember, this fluid, or hemolymph, circulates in large body spaces, not in closed vessels. The pressure which causes circulation also keeps the body "pumped up" thus giving it form, as with a balloon. So, when our predator punctures its food item and hemolymph rapidly spews out, the full caloric value of the prey goes unrealized. Because *B. gigas* cannot return to the drawing board to correct this problem, it gets busy groping for more prey to meet its energy needs, and grope effectively it does! Anderson (1970) demonstrated this fact with a simple and tidy experiment in which he placed 1,040 cladocerans, 200 copepods, and 20 *B. mackini* in 3 L of water with a single 75 mm-long *B. gigas* female. After 200 hours in this dark, 10°C meat market, only the female predator was left swimming.

Perhaps when food resources become scarce *B. gigas* casts around for alternatives; at least Fryer (1966) thinks so, for he suggests that scraping is used to supplement its diet. And just so you know this beast seems to take advantage of every option to enjoy a meal, Belk and Ballantyne (1996) observed some of these characters clustered around a wad of *Spirogyra* apparently "...pulling at the algal mass with their phyllopods." That they feed on this kind of material at times is suggested by the fact that algal filaments were found between the mouth parts and in the gut. Those times must be few, however, for as we have noted, *B. gigas* typically lives in waters so turbid that algae cannot grow.

What eats fairy shrimps?

The old adage that "those who live by the sword, die by the sword" even has meaning for anostracans. Although these graceful and seemingly passive creatures are hardly the sword-carriers for which the statement was written, they do live by eating considerable quantities of living things. And, in their turn, they die by the "swords" of birds, bugs, and beetles. Some also fall prey to jaws of relatives – another fairy shrimp or a tadpole shrimp, even dragonfly larvae, occasionally fish, amphibians, and, yep, humans. About who eats them from the inside (parasites) we know next to nothing except that they do fall prey from within. Amat *et al.* (1991) and Jarecka (1984) noted that the brine shrimp *Artemia*, and the freshwater fairy shrimp *Branchinecta gaini*, can serve as intermediate hosts for the cyst stages of hymenolepid tapeworms. The presence of these cysts has no effect on survival, but it does lead to castration, obviously a factor in the size of the next generation of shrimps. Long-time anostracan enthusiast Robert Brown collected a pot full of *Branchinecta lindahli* near Soda Lake in San Luis Obispo County and returned them to his lab at CSU San Luis Obispo. There he watched as an unknown micro-organism grew and occluded the anostracans' body cavities. Once filled with whoever it was, the fairy shrimps succumbed. As has been said before, there needs to be bread on every table!

So much for pleasantries, let's get down to naming names of those who eat whole fairy shrimps! How's this one: **giant fairy shrimp**, so named because it is! We just told you about this behemoth's eating habits, but feel free to check back on its culinary artistry.

Another predator of anostracans is the tadpole shrimp (Fig. 1.1, p. xiv). There are four species of these "Jurassic Park" creatures in our state. Three live in turbid, desert alkali playas like our giant friend *Branchinecta gigas*, the fourth dwells in pools of low dissolved solids in the northern Central Valley. Two of the desert alkaline-lake tadpole shrimps share the same food, *B. mackini*. However, they appear to divide feeding opportunities in these places by season. *Lepidurus lemmoni* eats *B. mackini* in winter and spring waters. *Triops newberryi* must "chow down" on them, possibly *Thamnocephalus platyurus* and who knows what else, during summer (no one has ventured into the heat of the Mojave at opportune moments to find out).

The intriguing question (yes, another question) is: how do *B. gigas* and *L. lemmoni*, whose distributions in California overlap significantly, divide winter and spring playa waters between them, given that they share *B. mackini* as their major food? Before the 1992-1993 rainy season we knew of no records that these species co-occurred, and we wondered who out there would find out why? Well, we still don't know why, but Marie Simovich and Richard Gonzalez (1993) found both species inhabiting sites scattered across Edwards Air Force Base in the Mojave Desert. In 8 of those pools, one species or the other was present; in 12 of them both occurred. However, in examining the Simovich-Gonzalez data, we noted that *B. gigas* was often present from November to January, while *L. lemmoni* did not usually appear until January or March and remained in the pools later into spring, in several cases much later. Perhaps thermal cues separate the hatching times of the two predators. When the earlier-hatching *Branchinecta gigas* appears, its nutritional needs are met by *B. mackini*. As the *B. gigas* populations bow out, *B. mackini* is then fed upon by the later-appearing *L. lemmoni*.

Lepidurus couseii has recently been recorded in the Great Basin Desert of the far north-east of our state, and although it has not yet had its eating habitats described, we'll bet it too eats anostracans.

Golly, desert waters seem to have phyllopod predators of fairy shrimps galore; but how about the rest of California? The fourth of the state's tadpole shrimps, *Lepidurus packardi*, dwells mainly in the northern and eastern Central Valley. Its distribution thus overlaps those of *Branchinecta lynchi*, *Linderiella occidentalis*, and several uncommon fairy shrimp species. In a Sugnet and Associates study (1993), *Lepidurus* was taken in 345 of about 3,100 locations checked, and at least 40 of these were occupied by *L. occidentalis*, many fewer by *B. lynchi*. Although we know nothing about the interactive private lives of these creatures, we must assume *Lepidurus packardi* enjoys eating tasty anostracans whenever they co-occur.

Other than those organisms exposed above, there are no others that prefer munching on fairy shrimps who dedicate their whole lives to pools. But, like children and relatives who take advantage of abundance, then leave when supplies run out, there are predators that fly, walk, hop, or swim into pools when such pastures are plentiful; then fly, walk, hop, or swim out (if possible) when pool resources dwindle or water disappears.

Studies with islands show the smaller the island, the fewer the colonizers that happen to find it and therefore occur there. In like manner, the more distant the island the fewer in number are the species in residence. Why talk of islands when our concern is puddles? Well, such places are aquatic "islands" in a sea of land, and if those pools are "next door" to permanent water, as is relatively common in the northern two-thirds of the Central Valley and the high Sierra, organisms which inhabit the latter find the pools in a short time. In areas where permanent water is scarce, and temporary pools are often quite distant from a permanent source, colonization is slower, possibly even out of the question for most species. A broad brush would paint California's southern mountains and deserts with this color.

Water birds, being highly mobile travelers, have got to be amongst the fairy shrimp's biggest concerns even in some of the most distant "islands". These birds are large and always hungry. They move easily into a habitat, take what they can get, then depart. In desert areas, American avocets are a particularly common sight wading in turbid, alkaline waters and swishing their sword-like beaks to and fro. Whatever they hit they attempt to grab. Given fairy shrimps' place in food chains, and thus their numbers, they are undoubtedly the most common morsels encountered by the avocet's beak. Kildeers, wading birds which also are known to eat fairy shrimps (Proctor *et al.* 1967), are a common sight around rain pools throughout California, and Lenz (1987) describes gulls and grebes as being avid eaters of Mono Lake's resident brine shrimp *Artemia monica*.

Swanson *et al.* (1985) and Eldridge (1990) have written that northern pintails and mallards, which come to rest on prairie pools along the midwestern flyway, feed on fairy shrimps because they are one of the first invertebrates available once the temporary waters form. Northern shovelers and blue-winged teals also are noted to have significant portions of their diet composed of anostracans. Undoubtedly these and other ducks that wing their way over California find fairy shrimps equally significant to their diet, but we are unaware of any research done in the state on the feeding habits of ducks. What we are aware of is that "The wetlands of the Central Valley provide wintering habitat for 19% of the wintering waterfowl in the continental United States. They support some of the highest densities of waterfowl in the country. Nationally, these are the highest priority wetlands for preservation of wintering habitat." (Secretary of Interior 1994). We also know that the Central Valley is California's richest fairy shrimp country. We suggest that these two facts are not unrelated! Further, an observational study of use by birds of vernal pools on the Santa Rosa Plateau in western Riverside County (Baker *et al.* 1992) demonstrated that, in the larger pools, mallards, northern shovelers, and northern pintails are frequent guests. In addition, green-wing and cinnamon teals are common, and the list goes on to include gadwalls, American wigeons, and ring-necked ducks. Since the waters of these larger pools are plied by fairy shrimps, we doubt the ducks come merely to float unaware of the shrimps' presence. For more information on avian uses of California's ephemeral pools, take a look at the review by Joe Silveira (1998).

Although insects are reasonable fliers, distance from their permanent-water refugia to temporary pools becomes a problem. Only adult insects fly, so they are the colonizers, and aquatic bugs and beetles are the most common of these. Having flown into the soup of a pool, they spend their time diving, often to some depth, in search of prey. Of the bugs, the most common are backswimmers (Family Notonectidae). Like all bugs, these have mouth parts for piercing their prey and sucking it "dry". Notonectids are aqualungers, so they may be seen hanging from the surface film where they recharge their air stores, then dive after food, including fairy shrimps. And eat fairy shrimps they do, at the clocked rate of 2.06 individuals per notonectid per hour (Woodward & Kiesecker 1994).

Predaceous diving beetles are another common sight. Like the bugs, they too carry an air store and also hang from the surface film, then swim rapidly through the water in search of prey! There are a variety of species and sizes, but some fall into the size range of anostracans, and some are even much larger, both as larvae and adults. Although both life stages feed in the same manner, larvae are particularly fascinating beasts. The mandibles are magnificently large, curved, and sharp. In fact, they are hollow and are not used in chewing. Like ice tongs, they close on their prey and impale it. Then digestive enzymes are pumped into the body of their food through these hollow structures and, when digestion has reduced the prey's internal parts to a slurry (exoskeletons are not digestible), it is sucked in through the beetle's mouth with gusto. Bob Brown points out that if the beetle is in no hurry, meaning that it must make the most efficient use of limited food reserves, this feeding strategy is a tidy way to go. However, he has watched many a diving beetle grab, pierce, suck, and run (swim off), suggesting that if food resources are plentiful, sucking a fairy shrimp's hemolymph, rather than waiting around for digestive enzymes to reduce tissue to a slurry, is the more efficient way to proceed.

If the pool is long-lived enough, offspring of these air-breathing colonizers may be seen in numbers, as may the aquatic larvae (also called nymphs or naiads) of dragonflies and damselflies. Adults of the latter groups are terrestrial insects, and are seen flying in the vicinity of pools looking for food and mates, but they are also there to lay eggs in the water. Because the larvae are aquatic and have gills, they always remain submerged, usually clinging to a surface, be it the bottom or aquatic vegetation. Although they move from place to place, they are not great swimmers like beetles and bugs, and thus are more the wait-see-and-pounce type of predator, some pouncing on fairy shrimps.

All these predatory insects must see to feed. Should the pools become occluded, vision is impaired, their way of life is obviously limited (Woodward & Kiesecker 1994), and these creatures disappear. Another way of saying this is that, if pools are muddy, visual predation is out of the question, and finding prey by bumping into it is "the way to go"! So we have come full circle in our feeding story; we are back to fairy shrimps and fairy shrimp-relatives eating fairy shrimps in the darkness of muddy pools! One last comment though about such environments. Because this bump-and-feed life style not only depends on a high density of prey but a large enough prey population to support a predator population, small pools and puddles, particularly those with small numbers of anostracans, do not sustain the predator level of this food chain. However, should the small pool be clear, it may also contain the visually-feeding bugs and beetles who can snatch up conspicuous and tasty morsels, then leave to gain sustenance elsewhere.

We have an uncommon but wonderful little example of free-market opportunism to share with you, although it is certainly insignificant to fairy shrimp biology. Our story involves a midge, a relative of the mosquito. As larvae, midges, like mosquitoes, are aquatic. Unlike mosquitoes they don't hang from the surface film; rather, they live on or just under surfaces, usually of the bottom sediments. And also unlike mosquitoes, some of them are predators. Anyway, Tim Graham (1994), a U. S. Biological Service scientist, was peering into potholes (the water-filled variety) in Utah when he noticed a fairy shrimp moving about erratically. "Good reason for such panic", he undoubtedly thought when he saw a midge larva clamped on the fairy shrimp's head. Because midge larvae are usually somewhat buried in bottom sediments, and fairy shrimps swim, little is the opportunity for such a predator-prey interaction to occur. Knowing this, Tim monitored the encounter until the midge had killed and consumed half of the fairy shrimp. How did a swimmer cross paths with a non-swimmer? Perhaps you will remember that some species of fairy shrimps have a habit of mucking around (scraping) in bottom sediments. Undoubtedly Graham's fairy shrimp was following that passion when the midge trap was sprung. Perhaps a more orthodox paraphrase of a common expression is appropriate here: "predation happens"!

As mentioned in the "Community" section of Chapter 3, fishes may occasionally enter anostracan habitats when flooding occurs, be it natural or agricultural. McCarraher (1959), Pereira and Gonzalez (1994), and Zemmouri (1991) have caught various fish species in the act and recorded it for posterity. When such an event occurs, the opportunistic fish will certainly eat fairy shrimps until they cannot find more, until they find their way out, or until they perish with the pool's drying. We can safely say that fishes are of little importance to modern-day fairy shrimp ecology; however, in the vast past of evolutionary time, after fishes first came into being, they must have encountered environments filled with tasty fairy shrimps. Kerfoot and Lynch (1987) and Wägele (1992) reason that the evolution of more versatile predatory methods by fish (read this over-kill by fish), particularly the development of suction feeding, ultimately exterminated fairy shrimps from all permanent waters by Mesozoic times, leaving anostracans only ephemeral pools as refugia against extinction.

Frogs, toads, and salamanders are also not usually thought of as inhabitants of temporary waters. However, in damper areas of California, and in wetter weather, adults of these creatures may migrate to pools to lay eggs, and, along with their immatures, use these wet places as temporary feeding sites. Frogs feed both above and below waterline, and how effective they might be in utilizing fairy shrimps is unknown, but instances of young bullfrogs filling their guts with tadpole shrimps are known from the Vina Plains near Chico (Federal Register 1994). Anostracans are a part of the diet of at least some salamanders and their larvae. We say this, even though no one has gone public with such information from California, because several scientists have spied on these beasts elsewhere (e.g., Sprules 1972; Thiery 1991; Woodward & Kiesecher 1994; Woodward & Mitchell in prep.) and found both adults and immatures to include fairy shrimps in their food supply. Finally, in California's more southern reaches where spade-foot toads hang out, they and their sometimes predaceous tadpoles may benefit from fairy shrimp feasts. Although no one has told of this drama being played out in California either, once more we rely on Woodward and Mitchell (in prep.) for the juicy information that adult spade-foots will in fact feed on *Streptocephalus texanus*. Interestingly, tadpoles of the spade-foot toad come in both predator and omnivore morphs (forms), sometimes in the same pool. In a fascinating piece of work by David Pfenning (1990), via astute observations and experimental manipulations he showed that "...morph determination depends on the ingestion of shrimp.... If a critical number of shrimp were ingested, the tadpole developed into a carnivore; if not, the tadpole developed into an omnivore." And who were these body-building New Mexican "shrimps"? Ah, those tasty tid-bits (steaks?) *Streptocephalus texanus* and *Thamnocephalus platyurus*, that's who. By the way, Simovich *et al.* (1991) also agree that fairy shrimps are "...an important component of the natural diet..." of spade-foot toad tadpoles in Arizona; so this issue seems to be settled!

The last of the vertebrate predators, with collecting equipment and behaviors capable of sampling both turbid and clear waters alike, are humans. Among them of course are those of us who study fairy shrimps, as well as the individuals who use these graceful creatures for the myriad of purposes already revealed in the Chapter 1 section "What good are fairy shrimps?"

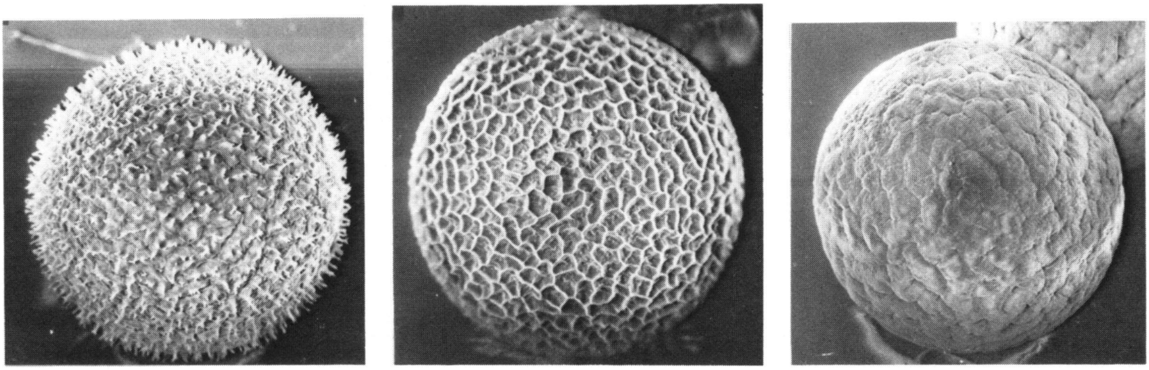

Fig. 3.2. Cysts of the California species of *Eubranchipus*. From the left, *E. serratus* 0.38 mm diameter cyst, *E. oregonus* 0.37 mm diameter cyst, and *E. bundyi* 0.31 mm diameter cyst. SEM photographs by Graziella Mura, Università degli Studi di Roma "La Sapienza", Italy.

Chapter 4

STATEWIDE DISTRIBUTION OF FAIRY SHRIMPS

Fairy shrimps aren't everywhere in California

California is certainly rich in anostracans. In fact, we can rightfully brag that, of the 23 known species that call our state home, eight are found only here (and in a northern sliver of Baja California, Mexico). These statistics are both North American and world records for the number of species of anostracans occurring in a comparable land area. No matter the reality, we sometimes hear silly and uninformed rhetoric about fairy shrimps on radio and TV by individuals hoping to harvest political hay. The printed page may be no different, as exemplified by the grossly inaccurate, almost hysterical disservice to truth by some unidentified author of a Wall Street Journal article dated October 17, 1994. The thesis of the article, entitled "A Fairy Shrimp Tale", was that all shrimps are the same, and all live in mud holes, and because mud holes are everywhere, fairy shrimps are everywhere. Ignorance is bliss they say, but in spite of this writer's bliss, **FAIRY SHRIMPS AREN'T EVERYWHERE!**

True, we have described our little subjects as "the symbol of rain pools", but they are not in every rainpool, or mud puddle, or stock-watering hole, or road-side ditch, or even everywhere in California as is attested to by Map 4.1 (p. 58), a compilation of all known locations of all of our state's fairy shrimps! Don Wootton used to tell your first author that even in the heart of the Central Valley's fairy shrimp country he could find no anostracans or tadpole shrimps west of the Sacramento River from Yolo County north. An intensive survey by Sugnet and Associates, Roseville, (1993), apparently blanketing all of the Central Valley and beyond, and including private lands often difficult to sample because of limited access, led to essentially the same conclusion. Further, they found the same general absence of anostracans and notostracans in the Central Valley west of the San Joaquin River from Alameda County south. Shawn Gallagher (pers. comm.) wrote of his impression of few fairy shrimp locations west of the Sacramento River when he sent us an unpublished "Vernal Pool Survey" (Alexander & Gallagher 1993), done while he was a student at CSU Chico, demonstrating that of 36 pools visited west of the river and south of Red Bluff only 10 contained shrimps, all *Branchinecta lynchi*. One might argue that there are few fairy shrimp sites west of the Central Valley's two main rivers because development has "done'em in". However, there is no less development east of the rivers where the great majority of the Valley's anostracans are found, so this is an unsatisfying suggestion.

Finding out what species reside on the less developed lands of wildlife refuges, no matter their location, would be a worthwhile endeavor since historically these places have gone largely unexplored. To its credit, the Federal Government has recently developed an interest in wetlands, and fairy shrimps, so managers of National Wildlife Refuges (NWR) have begun to look for species

Map 4.1. Plot of all our records of occurrences of fairy shrimps in California.