DESERT BIOLOGY

SPECIAL TOPICS ON THE PHYSICAL AND BIOLOGICAL ASPECTS OF ARID REGIONS

Edited by

G. W. BROWN, JR.
COLLEGE OF FISHERIES
UNIVERSITY OF WASHINGTON
SEATTLE, WASHINGTON

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CHAPTER IX

DESERT LIMNOLOGY

Gerald A. Cole

> *"Behold, I will do a new thing; now it shall spring forth, shall ye not know it? I will even make a way in the wilderness and rivers in the desert."*
> Isaiah 43:19

I. Introduction

Because of the distribution of certain closed lakes, the limnologist is forced, with some misgiving, to accept a broader definition of desert than might please a terrestrial ecologist. He must consider, e.g., the permanent, saline lakes of southern Saskatchewan, lying in a Park Belt savannah (Rawson and Moore, 1944) as well as Australia's Lake Eyre, a tremendous playa, dry for decades and surrounded by parched, inhospitable land, because, in hydrographic terms, deserts are defined as regions where no runoff reaches the sea. This links areas where annual precipitation is 50 cm or more with those receiving less than half as much (Fig. 1). Closed-basin lakes can occur only where gross evaporation substantially exceeds precipitation, and this correlation prevails in tracts that are not desert in every sense; some semiarid steppe regions would be covered by the definition. In the United States, the easternmost closed basins are in North Dakota near the boundary of the dry and humid climates that runs southward through Oklahoma and central Texas (Thornthwaite, 1948).

It is evident from Fig. 1 that anomalies occur in the climatic distribution of some major desert waters. For example, the Salton Sea, California, and various permanent waters of the Cuatro Ciénegas basin, Coahuila, Mexico, occur in regions where there are many temporary pools and playas. In these instances the provenance of water takes on special significance. The Salton Sea continues to exist as a limnological feature only if additional water is diverted into its basin to compensate for evaporative loss, in the neighborhood of 2 meters per annum (Blaney, 1955). Extensive waters in the Cuatro Ciénegas basin rise from deep subsurface aquifers and are, therefore, permanent.

Diversity in desert waters is to be expected, of course, but despite this they share a great number of features. Throughout the world there are equivalents on the different continents, and it is these counterparts and other similarities that are to be emphasized.

Continental arid-land waters are markedly influenced by climatic fluctuations that may be of minor importance in more humid regions. A result is the high incidence of astatic lakes and their precarious existence. In drier regions complete desiccation of lakes may follow a decline in precipitation or a temperature rise that increases evaporation and reduces runoff. Closed lakes in more humid regions are also delicately poised—an increase in precipitation might make them open lakes and thus remove them from the realm of desert limnology.

In endorheic or arheic zones, waters are typically concentrated, are high in electrolytes, and are quite different from the dilute, standard type

(Rodhe, 1949) of humid, exorheic areas. Waters may undergo different chemical evolution, however; some become sodium chloride waters, much like concentrated seawater or brackish water, and are termed thalassohaline. Others are athalassohaline, being quite different from seawater in relative ionic content.

Especially interesting are the physiographic parallelisms in the major

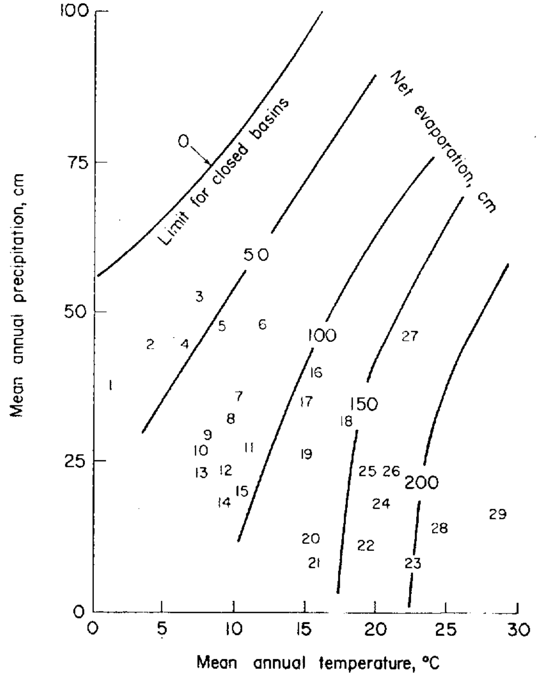

Fig. 1. Closed-basin lakes in relation to some climatic factors. Modified from Langbein (1961). Key: (1) Saline lakes of Sakatchewan; (2) Devils Lake, North Dakota; (3) Lakes of the Flagstaff region, Arizona; (4) Nebraska potash ponds; (5) Llano Estacado playas, Texas, theoretical Pleistocene conditions; (6) Llano Estacado today; (7) Great Salt Lake, Utah; (8) Abert Lake, Oregon; (9) Grants Lava Bed, New Mexico; (10) Pluvial Lake San Augustin, New Mexico; (11) Long-H Ranch salt ponds, Arizona; (12) Hot Lake, Washington; (13) Moses Lake, Washington; (14) Soap Lake and Lake Lenore, Washington; (15) Mono Lake, California; (16) Peña Blanca Lake, Arizona; (17) Bottomless Lakes, New Mexico; (18) San Carlos Reservoir, Arizona; (19) Willcox Playa, Arizona; (20) Salton Sea, California; (21) Owens Lake, California; (22) Waters of Cuatro Ciénegas, Mexico, and Lake Mead, Arizona; (23) Dead Sea, Israel; (24) Ponds of the Salt Desert, Iran; (25) Little Triste Represo, Arizona; (26) Quitobaquito limnocrene, Arizona; (27) Lake Tiberias, Israel; (28) Lake Eyre, Australia; and (29) Temporary ponds at Khartoum, Sudan.

deserts of the world. Inland seas either formerly occupied most of such deserts or are now present as exemplified by the Caspian and other seas in Asia, Great Salt Lake in North America, and Lake Eyre in Australia. The Great Australian Rift includes the immense playa, Lake Torrens, once a part of the Spencer Gulf but now 60 km away. Its similarity to the African Rift and the relative positions of the Dead Sea and Red Sea is obvious. In North America, the Salton Sea lies below sea level in an elongate depression once continuous with the Gulf of California, a situation reminiscent of the Dead Sea and the Red Sea.

Thermal springs also are major habitats in almost all desert basins of North America, Asia, Australia, and elsewhere. They demonstrate, perhaps, another extreme when compared to large, closed lakes. The province of desert limnology becomes complex, indeed, with the inclusion of springs, desert streams, and both permanent and ephemeral standing waters.

II. Physical Features

A. Provenance of Desert Waters and the Climatic Distribution of Lakes

Precipitation on lake surfaces in arid deserts can be practically ignored as a water source; it may be relatively important for lakes, especially large lakes in more humid climates. Precipitation within a desert drainage area, on the other hand, can be of extreme consequence. Seasonal or irregular storms convert normally dry channels into torrential streams or send sheets of water across the desert floor to fill depressions that may have been empty for many months. Such flashflooding creates only transitory streams; the region is essentially arheic, one in which no rivers arise. Its streams and lakes are extremely astatic. A varied terminology describes comparable situations in different deserts. The dry wash or arroyo of North America is the African *wadi;* the dry salt playa is the Iranian *kavir,* the *barrial* of Mexico, the Chilean *salar,* or the *chott* of North Africa.

In parts of the American Southwest, as in other desert areas, the storms often are localized so that one depression fills while a nearby basin in a different drainage pattern remains dry. The filling and desiccation of many natural playas and *represos,* the American cattlemen's tanks, are characterized, therefore, by irregularity. In areas where seasonal rains are widespread and heavy, playas have a more or less annual cycle, acquiring their water via runoff. The importance of large drainage area is exploited in constructing dams to impound stock waters; the successful represo is placed so that a maximum area drains toward it and it receives the runoff from several showers each year.

In addition to total drainage area, any other of several factors affecting runoff is important. Evaporation seems to be the master factor. Reeves (1965) concluded that Pleistocene precipitation on the Llano Estacado of west Texas may not have been much different from today; the existence of Pluvial lakes in basins that are now ephemeral playas (Fig. 1) depended on lower mean temperature, reduced evaporation, and the resultant increased runoff.

Permanent influents reach other desert basins of internal drainage, terminating there in saline lakes. In such endorheic regions the lakes approach permanency but are still characterized by astatic levels. Lacustrine morphometric parameters play a role here. The Great Salt Lake, Utah, and its Iranian counterpart, Lake Urmia, are fed by streams; these shallow bodies are alternately swollen and shrunken by flood and drought. The deep (104 meters) Pyramid Lake, Nevada, in the endorheic Lahontan Basin, maintains a more nearly uniform level. Neither type shows the extreme astacy, e.g., of Lake Eyre (Fig. 2). No lakes are formed in endorheic regions where adequate basins are lacking; noncontributory rivers disappear below the sand or evaporate before reaching the sea.

It appears contradictory that a large river flowing through an arheic zone may be part of the desert scene. This happens when a river arises in a more humid, exorheic locale and flows through arid deserts en route to the sea. Typical examples are the Colorado and its major tributary, the Gila, now barely rivers because of the many impoundments along their courses. The lower Nile is another example.

Seepage water entering the lake through the basin wall has recently diluted such desert lakes as Soap, Washington (Anderson, 1958a), and Big Soda Lake, Nevada (Hutchinson, 1937b). The upward movement of ground water into shallow basins is a common occurrence in some regions, and ground water emerging from distinct springs creates lakes in other arid regions. The extensive surface waters of the arid Cuatro Ciénegas bolson in Mexico all originate from springs (Minckley and Cole, 1966). The daily flow of spring water may be almost negligible, as in the Long-H salt ponds, Arizona, where the trickle from an aquifer may not reach them during the height of summer (Cole and Whiteside, 1965b), or as great as the 5600 meters^3 of water entering Montezuma Well, Arizona, each day from fissures 17 meters below the surface (Cole, 1963). This daily income is of the order of one tenth the volume of the pool.

Figure 1 shows the distribution of some desert waters plotted in relation to climatic factors that determine net evaporation. Net evaporation, as

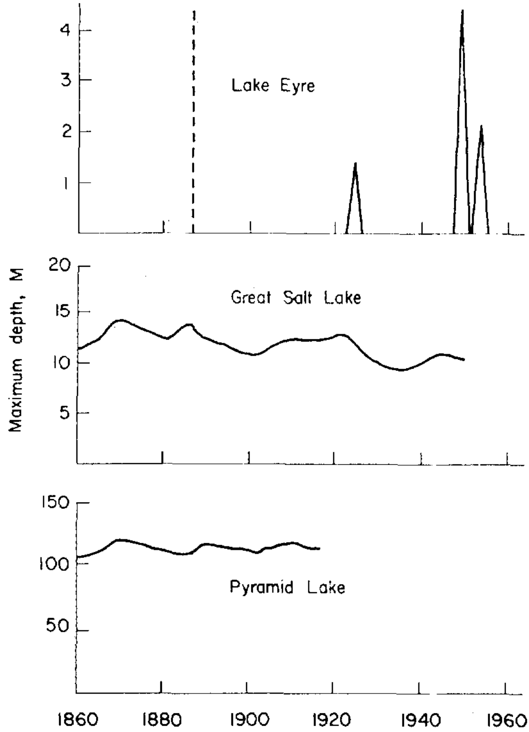

Fig. 2. Fluctuations in surface level of three types of closed-basin lakes. Modified from Langbein (1961).

defined by Langbein (1961), is the difference between evaporation and precipitation on the lake. There are no closed basins plotted in areas with annual precipitation of much more than 50 cm, and there is none near the theoretical climatological limit for closed basins where the net evaporation is zero. Frequent overflows caused by erratic fluctuation in precipitation would occur at this theoretical limit, and the basin then could not be considered closed. The lakes plotted in the area between zero and the line where net evaporation is 50 cm (Fig. 1) are permanent and are best described as steppic or prairie rather than desert lakes.

Between net annual evaporation rates of 50 and 100 cm there are several important arid-land waters (see Fig. 1). Here lie several closed basins with stream or subterranean influents and some impermanent playas.

Where the combination of precipitation and temperature results in 100–150 cm annual net evaporation (Fig. 1), there are some playas that are rarely filled (e.g., Owens Lake, California, and Willcox Playa, Arizona). Exceptions include astatic impoundments fed by intermittent-stream drainage systems and waters fed by subsurface seepage such as the Bottomless Lakes, New Mexico. Where the net evaporation is greater than 150 cm per year, the lakes are mostly ephemeral except for those with artesian sources, such as the Cuatro Ciénegas waters or the river-fed Jordan Valley lakes (Fig. 1).

B. ORIGINS OF DESERT LAKE BASINS

A detailed and systematic account of lakes based on method of origin includes 76 divisions of 11 major types (Hutchinson, 1957). At least 7 types are represented by desert lakes. A brief discussion of the agents involved in the geneses of desert lakes follows.

Wind action is treated first because aridity seems to be necessary for aeolian construction or modification of lake basins; thus, this agent is unique to desert regions. Shallow deflation basins, most existing as impermanent playas, are widespread in arid lands and are part of the desert scene. Those which hold permanent water probably reflect climatic change since they were first excavated. Shallow, wind-scoured depressions, called "gobis," are a topographic feature of the great Asian desert deriving its name from their abundance.

The pans of the Transvaal (Hutchinson *et al.*, 1932) and the *chotts* of North Africa (Gauthier, 1928) have received some limnological attention. The playas of the Llano Estacado in Texas are circular bodies reminiscent of the South African pans. In the Kalahari Desert of Africa there are also many pans. Deflation basins, or large structural depressions modified by wind action, occur in the arid central region of Australia and in the Seistan region of Iran.

The origins of aeolian basins are probably complex. There are about seven types of playas in the Llano Estacado (Reeves, 1962), although deflation has had a role in molding most of them. Ungulate action has probably played a part in the removal of material from the African pans and the Llano Estacado lakes, and elephants may be involved in the fashioning of some Kalahari pans (Debenham, 1952).

In addition to deflation, wind action has created lakes by piling up dams of sand—the soda waters of Moses Lake, Washington, e.g., are impounded by a dune (Russell, 1895). The many Sandhills lakes of Nebraska occupy depressions bounded by dunes that are fairly stable at present; some *erg* regions of the Sahara contain waters, but most of these are too arid for lakes in spite of favorable wind-shaped topography.

From the standpoint of numbers and limnological endeavor, tectonic lakes rank high in desert limnology. Seas of the Caspian complex, and some lakes of the Lahontan Basin in western North America, occupy tectonic depressions. The Caspian Sea and the Sea of Aral were formed by epeirogenetic uplift, and the Lahontan lakes are in grabens (Hutchinson, 1957). The whole complex rift system from the Jordan Valley through the Red Sea into Africa includes lakes of general limnological interest; many, such as the lakes of the Jordan Valley and certain African waters—e.g., Lake Rudolf—lie in desert lands. Many tectonic basins in North America once contained vast pluvial lakes (Hubbs and Miller, 1948); now there are astatic remnants, such as Great Salt Lake, Utah. The basin of Cuatro Ciénegas in the state of Coahuila, Mexico, once contained one or more lakes; other large bolson lakes, now mostly dry, occur in Mexico.

Lakes occupying depressions formed by various volcanic activities are among the most important in desert regions. Noteworthy limnological contributions come from Big Soda Lake, Nevada (Hutchinson, 1937b), and Borax Lake, California (Wetzel, 1964); many geologically oriented papers have come from studies on the alkaline Mono Lake, California. Specialized aquatic habitats in the Grants Lava Bed, New Mexico, have been investigated by Lindsey (1949, 1951). There are probably many small volcanic lake districts in arid regions awaiting study. The lakes around Flagstaff, Arizona (Fig. 1), may be typical of these (Cole, 1963). Some occupy depressions in lava flows and calderas; lava dams and cinder cones impound others.

There are relatively few examples of fluviatile basins in arid realms, but their limnological importance is great because of the important papers by Edmondson (1963) and his students dealing with the plunge-basin and eversion lakes of the Grand Coulee, Washington. Unexplored minor fluviatile habitats in the American Southwest are the *charco* and *tinaja,* temporary pools occurring along stream channels. The former appears after flood water spreads out over adobe flats, and the latter consists of rock pools scoured in desert canyons. The charco is represented in Africa by the *toiche,* a Nilotic term for riverain areas flooded by the White Nile (Rzóska, 1961).

Glacial activity has produced comparatively few lakes in arid regions, yet much information on desert limnology has come from glacial lakes because of the important studies of Hutchinson (1937a) and Rawson and Moore (1944) on the lakes of Indian Tibet and Saskatchewan, respectively.

Man-made impoundments of various types are exceptionally important because of their abundance. In the American Southwest small earthen impoundments, *represos,* are very numerous, but there is no consequential literature on them. More is known about their African counterpart, the *barrage,* because of experimentation by fish culturists. Limnological literature has come from larger impoundments such as Lake Mead on the Colorado River (Anderson and Pritchard, 1951) and Elephant Butte on the Rio Grande (Ellis, 1940).

Human activity is partially responsible for the Salton Sea in southern California. It occupies a natural depression separated from the Gulf of California by delta deposits, and large Pluvial Lake Cahuilla preceeded it. Accidental diversion of irrigation water into the dry basin in the early 1900's is responsible for the modern lake (Carpelan, 1958).

Little study has been directed toward the solution basins in arid regions. The Bottomless Lakes, New Mexico, Montezuma Well, Arizona, and some lagunas in Coahuila, Mexico, are American examples of this type.

Meteoritic impact craters are present in arid parts of Australia, Texas, Arizona, the Arabian Peninsula, and elsewhere, but none contain water now, although their sediments bespeak a lacustrine past.

C. Special Depositional Features

In many desert areas, especially in regions where Pluvial lakes once existed, there are remarkable masses of precipitated material. The curious formations in the desert south of the Dead Sea may be the most famous, various ones having been identified as the wife of Lot (Lane, 1948). Many mound springs in the Great Australian Artesian Basin have collapsed and evolved into limnocrenes, but others still stand (Williams, 1965a). In the Cuatro Ciénegas basin, numerous calcareous mounds, limnocrenes, and rheocrenes suggest the Australian situation (Minckley, 1965a). In desert valleys of Utah and Nevada there are tufa mounds, a meter or more high and holding water near the boiling point (Russell, 1895).

At the southwest end of the California playa, Searles Lake, a series of steep calcareous crags known as the Pinnacles rise 30 meters above the dry basin. In addition, an exceptionally massive reef of trona ($Na_2CO_3 \cdot NaHCO_3 \cdot 2H_2O$) stands at the east and northeast of the main playa (Gale, 1914). The tufa crags and towers at Mono Lake, California (Dunn, 1953), and the large formations at Pyramid Lake, Nevada, are well known (Russell, 1895). The blue-green algae, *Calothrix, Phormidium,* and *Nostoc,* were important in precipitating these calcareous deposits. Other methods may involve precipitation accompanying evaporation and mechanical action at the shoreline and precipitation from saturated hot-spring water entering colder lake water and in bottom muds from hot, supersaturated waters rising from below. The last method may result in more or less symmetrical domes.

Russell (1885, 1895) described the tufa zonation at the beach marks of Pluvial Lake Lahontan. A thick lithoid terrace that is compact, stony, and granular is at the highest level. A zone of dendritic tufa lies below it; this is the material composing much of the Searles Basin Pinnacles (Gale, 1914). A thinolitic terrace of well-defined crystals lies below the other two. Dunn (1953) found that most tufa towers at the orifices of what once were, or are now, sublacustrine springs at Mono Lake have a lithoid core with outer concentric and alternating dendritic and thinolitic layers. He suggested that much lithoid material at the shoreline is deposited at the contact of rainwash and lake water, and that mixing waters, rather than agitation, is the origin of this. The dendritic and thinolite tufa may be the result of either solution and redeposition within masses or of varying rates of deposition on the outside of the tower.

At the shores of Great Salt Lake, Utah, there are hectares of oölitic material deposited on sand grains and gelatinous masses of blue–green algae that form tufalike deposits (Flowers, 1934). The oölitic material suggests the lithoid material of the Lahontan Basin. Carozzi (1962) stated that *Aphanothece packardi* is the alga involved in the formation of the calcareous biostromes that are especially abundant on the east shore. *Pleurocapsa* also occurs in smaller numbers (see Bradley, 1963). The algae have no typical growth pattern, but they reproduce and emphasize the underlying topography carved in firm argillaceous and oölitic sands. The algal masses occur down to a water depth of 4 meters.

Travertine Rock at the northwest end of the Salton Sink, California, is 100 meters high and is encrusted by at least 50 cm of travertine. This rock mass, and Pumice and Obsidian buttes to the south, projected several meters above the waters of Pluvial Lake Cahuilla, or Lake LeConte, from which the tufa was derived (Jones, 1914). Because these were obstacles to waves and maximum turbulence occurred there, Arnal (1961) theorized that agitation and subsequent loss of CO_2 brought about the precipitation of calcium carbonate. This is reminiscent of a gorge near the shores of Lake Rudolf, where waterworn pebbles cemented by calcareous material form cliffs 30 meters high (Beadle, 1932).

Monkey Springs in southeastern Arizona has deposited a magnificent travertine plain that covers several hectares. This was formed before the spring effluent was diverted into a small irrigation ditch. All stages of tufa formation can be seen today in the lower reaches of the ditch. The role of the moss, *Hygroamblystegium fluviatile*, is paramount in building leveelike walls and tunnels of stone, although the bryophyte may only serve as a wick from which water is evaporated.

Many travertine terraces are seen below the Arizona Mogollon Rim just above the desert (Feth and Hem, 1962). Of these, the large inactive terrace at Fossil Creek is most noteworthy.

The waters that occur now in the vicinity of the deposits listed above are chemically diverse. According to the terminology of Clarke (1924), the California and Nevada waters are chlorocarbonate types except for Mono Lake, which is a good example of a triple water type. Lake Rudolf is a sodium carbonate type, and the Mogollon Rim springs are carbonate waters high in calcium. Monkey Springs has little sodium and chloride but is particularly high in calcium and sulfate. The Cuatro Ciénegas waters range from sulfatocarbonate to sulfatochloride types. Pluvial Lake Cahuilla may well have been dilute triple water, and the Australian waters contain much sodium chloride.

The singular importance of the sediments derived from pluvial lakes in arid regions to the study of paleolimnology and paleoecology is emphasized in the reviews by Bradley (1963) and Martin and Mehringer (1965).

D. THERMICS AND DENSITY RELATIONS

1. Annual Cycles

Various annual temperature regimes occur in desert lakes, although a great many are shallow and do not show stable stratification in any season. Warm monomictic lakes result from impoundment in the narrow canyons of the American Southwest (Cole, 1963); many of the deeper natural lakes in arid regions are monomictic. Dimixis results from impoundment at higher altitudes or latitudes. Meromixis is relatively common; Edmondson (1963, Table 13.1) listed eight known meromictic lakes of the western United States, seven of which are in arid regions. Beadle (1932, Fig. 5) presented some evidence for polymixis in Lake Rudolf, Africa, during at least part of the year; a weak diurnal stratification was destroyed by nocturnal cooling.

There are difficulties in precisely defining some of the annual cycles. For example, some meromictic lakes such as Hot Lake and Soap Lake, Washington (Anderson, 1958a,b), have ice covers of some duration—they are then temporarily amictic, as are normal dimictic lakes in winter. Melting of the ice, however, leaves clearly defined meromictic lakes in the Washington examples. The twin salt ponds at the Long-H Ranch in Arizona exhibit an unusual monomixis (Cole *et al.,* 1967). They become temporarily meromictic during the winter when evaporation is reduced and runoff introduces a dilute surface layer of water. Later in the year, evaporation reduces the volume of the ponds until they become isothermal and of uniform density, therefore circulating during midsummer. This is the reverse of what happens in a warm monomictic lake where thermal stratification is brought about by summer air temperatures and winter circulation is initiated by autumnal cooling. Moreover, during cold winter nights an ice cover forms on at least one of the Long-H ponds, but it melts during the first few hours of insolation. This cannot be termed polymixis in the sense employed by Krumholz and Cole (1959) for the dilute, holomictic Tom Wallace Lake, Kentucky. In the Long-H pond the melting of ice results in a meromictic lake.

2. *Temperature Phenomena and Heat Sources*

The unusual temperature phenomena that have been reported about desert lakes are a function of salinity. Some of the saline Saskatchewan lakes (Rawson and Moore, 1944) exhibit summer vertical temperature profiles that, superficially, appear typical of temperate lakes of moderate depth. There is an important difference, however. High salinity depresses the temperature of maximum density, and vernal circulation takes place at unusually low temperatures. Summer stratification, therefore, traps very cold water below the thermocline. Hypolimnion temperatures below 0°C occur in Manito Lake waters during the summer because their maximum density is at — 0.3°C and the freezing point is — 1.1°C. The most saline lake, Little Manitou, has a freezing point of — 4.1°C but is not deep enough to stratify.

The meromictic Hot Lake, Washington (Anderson, 1958b), exhibits dichothermy, mesothermy, and poikilothermy during the course of a year. The Arizona Long-H salt ponds show the same phenomena plus isothermy (Cole *et al.,* 1967). Such anomalous stratification is compensated by salt in solution (Fig. 3) so that stability may be considerable in spite of temperature–density relations that imply instability.

Extremely abrupt temperature gradients are characteristic of many saline, desert waters that are inversely stratified. Data from an Algerian pond only 30 cm deep imply a vertical gradient of 0.4°C/cm (Beadle, 1943). At Hot Lake, Washington, there was a 19.6°C change between the depths of 1.0–1.5 meters, a mean rate of 0.39°C/cm. The Long-H ponds have gradients as spectacular as this on some occasions, and during February a change of 1.2°C was observed within a vertical distance of 2 cm in one of them.

Summer temperatures of 50°C prevail in the monimolimnion of Hot Lake, and water at 30°C has been observed beneath a winter ice cover (Anderson, 1958b). In the Long-H ponds mean temperatures of more than 20°C occur on winter mornings after the melting of nocturnal ice sheets. Direct solar radiation is the major source of heat in deeper strata

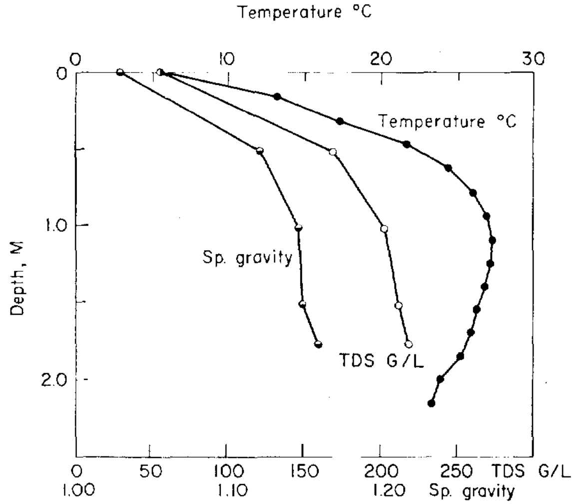

Fig. 3. Mesothermal temperature profile in Red Pond, Long-H Ranch, Arizona, showing the accompanying vertical stratification of total dissolved solids and specific gravity at the prevailing temperatures.

of shallow desert lakes that show such high temperatures there. Anderson (1958b) found that the observed daily temperature increase in subsurface Hot Lake was in close agreement with a computed gain based on light penetration. Dilute mixolimnion water lying above the saline layer allows the penetration of solar radiation but protects the lower stratum from cooling by evaporating. Also, because there is a minimum of mixing between the two layers, there can be little loss of heat from the deeper one except by slow conduction. In deeper meromictic lakes the source of monimolimnion heat is less obvious and probably accumulates slowly. Bacterial metabolism may be involved to some extent. In the sediments of the monomictic Lake Mead, Nevada-Arizona, heat accumulates from this source; Zobell *et al.* (1953) made a conservative estimate of the production of bacterial heat at the rate of 30×10^{-12} cal/cell/hour.

Paradoxically, in certain lakes of hot, arid regions the rate of heating decreases after the summer solstice more rapidly than does the rate of incoming solar radiation. In Lake Mead (Arizona–Nevada) and Lake Tiberias (Israel), a loss occurs before the summer solstice (Hutchinson, 1957). This is largely a function of the high evaporation rate from a warm surface.

Although evaporation is a cardinal factor in desert regions, loss of water by evaporation, of course, is reduced in waters of high salinity. Great Salt Lake, Utah, loses less than 100 cm, although in that climate

150 cm is the annual rate of evaporation from a freshwater surface (Adams, 1964). In the Long-H salt ponds from early June to mid-August about 300 cal/cm^2/day were involved in lowering the surface levels; in freshwater, 250 cal/cm^2/day would have sufficed.

3. *Heat Budgets*

The annual heat budgets of most desert waters are unknown, although some of the most nearly complete analytical heat and energy budgets have come from studies on desert lakes. These lakes are Lake Mead (Anderson and Pritchard, 1951), Lake Tiberias and the recently drained Lake Hula, Israel (Neumann, 1953), and the Dead Sea (Neumann, 1958).

Many desert waters are so shallow that heat exchange with the sediments must be great. Storage of heat in the monimolimnion of a meromictic lake may interfere with winter cooling. An annual heat budget of 2851 cal/cm^2 can be inferred from Anderson's (1958b) data for the shallow, meromictic Hot Lake. The even shallower Long-H ponds in Arizona have budgets of about 1000 cal/cm^2 (Cole *et al.,* 1967); a theoretical dilute, unstratified pond ranging from 4–25°C and of the same dimensions would have a calculated annual budget near 2500 cal/cm^2 if there were no sedimentary exchange. The meromictic Soap Lake, Washington, provides more acceptable data because it has a maximum depth of 27 meters. Its heat budget of 14,900 cal/cm^2 is unusually low for an unprotected, moderately deep lake, especially when compared to nearby, holomictic Lake Lenore, only 11 meters deep but with a budget of 16,110 cal/cm^2 (Anderson, 1958a). Desert monomictic lakes such as Mead, Tiberias, and Pyramid have budgets much like temperate first-class lakes throughout the world (Hutchinson, 1957, Table 53). Lake Mead, an impoundment on the Colorado River, receives a large percentage of its annual heat from the river (Anderson and Pritchard, 1951). Data from Arnal (1961) imply an annual heat budget of about 30,000 cal/cm^2 for the unstratified Salton Sea when it has a maximum depth between 13–14 meters. The annual heat budget of Montezuma Well, Arizona, calculated from coldest and warmest mean temperatures, is only 3600 cal/cm^2, although it lies in a region where winter temperatures below freezing are common. It receives more than 1800 cal/cm^2/day from subsurface influents and there is, therefore, relatively little winter cooling. The mean temperatures range from 19.1–24.5°C.

4. *Stability*

Stabilities of the meromictic lakes of deserts are great. Hutchinson (1937b) calculated about 60,000 gm-cm/cm^2 was needed to mix Big Soda Lake, Nevada, compared to 7640 gm-cm/cm^2 for the deeper, holomictic Pyramid Lake. The shallow (c. 2 meter) ponds at the Long-H Ranch, Arizona, have winter stabilities greater than 200 gm-cm/cm^2 when dilute runoff and melt waters overlie the dense, temporary monimolimnia (Cole *et al.*, 1967). These considerable stabilities are destroyed in midsummer when evaporation reduces the pond volumes about one fourth and lowers the surfaces more than 30 cm.

E. Optics

A most unusual feature of light penetration in arid-zone waters is the turbidity encountered in many. In some African pans, a small Secchi disc of about 6 cm diameter disappeared from 1.0 to 5.5 cm below the surface (Hutchinson *et al.*, 1932). In the permanent, but astatic, Little Triste Pond, Arizona, the annual mean of 25 standard 20-cm Secchi disc values was 6.0 cm (Barry, 1965). Subsurface photometer values meanwhile showed that an average of 99% of surface radiation was lost at the 20–25 cm level. No Secchi disc values as great as 1 meter were observed in the productive Salton Sea by Carpelan (1961), although Arnal (1961) reported a range of 0.1–3.05 meters and an extinction coefficient of 85%.

The source of turbidity varies. Aeolian detritus is certainly important in some regions, but Little Triste derives its turbidity from its basin and muddy runoff. From a boater's vantage, the Salton Sea appears gray to grayish beige because of sedimentary particles in suspension. Isopleths of turbidity follow the shoreline closely, suggesting a coastal origin, but contributions from the New River and the Alamo River at the south end are also involved (Arnal, 1961). Volcanic ash in the sediments is a source of turbidity in the windswept closed volcanic lakes near Flagstaff, Arizona.

Light penetration in other waters shows no unusual features. The annual mean photic depth in Peña Blanca Lake, Arizona, is 4.5 meters (Kemmerer, 1965). In the Arizona limnocrene, Montezuma Well, the mean photic depth is 9.4 meters, with little variation. The average Secchi-disc transparency is at the subsurface level where about 80% of the surface radiation has been absorbed, and the mean photic-zone-depth: Secchi-disc ratio is 3.0. No turbidity can be demonstrated in subsurface water samples from Montezuma Well.

Many briny ponds of the desert are red; in most instances chromogenic bacteria are responsible for this. An early report of bacteria cultured from the waters of Great Salt Lake, Utah, included three chromogenic species out of a total of five (Daniels, 1917). In shallow, stratified waters, purple sulfur bacteria often occur and are sometimes so close to the surface that they form a visible red layer (Lindsey, 1951; Cole and Whiteside, 1965b). In parts of New Mexico and other regions, where gypsum deposits are abundant, such rose-colored ponds are common. Also, dense populations of *Artemia* impart a red hue to some saline lakes.

III. Chemistry of Desert Waters

A. CONCENTRATION AND RELATIVE IONIC COMPOSITION

Changes in relative ionic composition that accompany evaporation in closed basins have been described by Clarke (1924) and Hutchinson (1957). A sequence occurs as the dilute spring, river, or runoff water is concentrated. The normal trend would be from carbonate to sulfato-chloride to chloride water as calcium carbonate and, later, calcium sulfate and perhaps sodium sulfate are precipitated. The relative increases of sodium and magnesium accompany the loss of calcium. In the extreme stages of concentration magnesium salts predominate over the less soluble sodium compounds, but bitterns of this type are not common. The Dead Sea, Lake Macdonnell in Australia, and the deep Kssyk-Kul in Turkestan are examples of magnesium waters. Hot Lake, Washington, contains magnesium water, but this is because it occupies a depression in epsomite ($MgSO_4 \cdot 7H_2O$). A theoretical terminal stage based on the extreme solubility of calcium chloride (Fig. 4) is the rarest of occurrences because

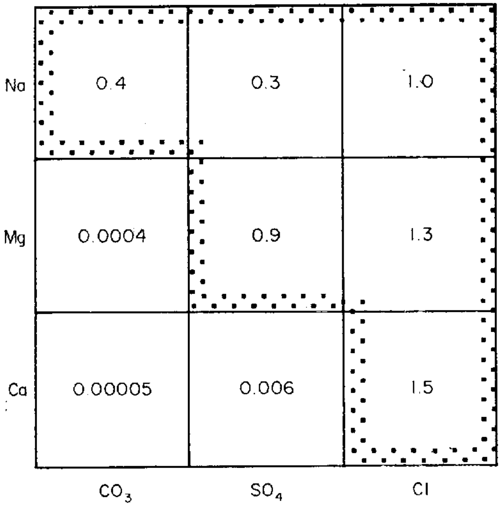

Fig. 4. Relative solubilities of salts in distilled water. (NaCl = 1.0 at 10°C.) Dotted border includes compounds predominant in closed lakes.

most calcium is precipitated earlier with carbonate and sulfate. For example, Loewengart (1959) calculates there are 5.4×10^{12} kg of $CaCl_2$ in the Dead Sea, and there would be three times as much if gypsum had not been precipitated en route from Lake Tiberias and the Beisan Springs. An exception to the above is Don Juan Pond in Victoria Land, Antarctica (Torii and Ossaka, 1965). This 10-cm deep body of water lies in a cold and extremely dry climate and is essentially a calcium–chloride lake. Needlelike crystals of calcium chloride hexahydrate, termed Antarcticite, occur in the water and on the bottom of the pond.

In general, as concentration proceeds there are decreases in the following ratios: Na : K; Ca : Mg; and Cl : Br. The last is of special interest. The Cl : Br ratio in seawater is about 288, but at the point of concentration where sodium chloride has precipitated, the ratio is about 34. The Jordan River has a Cl : Br ratio of about 280, but in Lake Tiberias the ratio is only 120 (Loewengart, 1959). This decrease in ratio is not caused by concentration and precipitation of chloride but by the contribution from the Tiberias Hot Springs that have a high bromide content and a Cl : Br ratio of about 73.

The total salt in solution and its concentration may vary greatly as volume changes occur in an astatic, closed lake. A schematic cycle for the salinity–volume relations proposed by Langbein (1961) cannot be compared in its entirety to actual data. A receding-volume phase, during which there is a net loss of salts from solution, and a rising-volume phase, when the mass of salt in solution is relatively stable, can be inferred from data collected in Devils Lake, North Dakota (Swenson and Colby, 1955). Data are not available on stable low-level and high-level phases when input of salt, in theory, exceeds the losses.

Salt fluctuations in an ephemeral playa are more easily demonstrated (Fig. 5). The dry playa includes a salt crust, thickest at the lower portion of the depression with its upper margin marking the level where salt precipitation commences during the shrinking, evaporating phase. When the playa fills, the salt crust begins to dissolve and total content and concentration increase as portrayed by the description by Mawson (1950) of turbid fresh rivers pouring into the saline Lake Eyre. If the water level rises above the salt line, the concentration decreases as the total in solution increases. Later, as the playa shrinks, the concentration increases, reaching saturation at the salting level and remaining relatively constant thereafter, while the total in solution decreases rapidly, as does the lake volume.

In spite of marked volume changes, the relative ionic composition of a saline lake remains singularly stable (Swenson and Colby, 1955; Bonython, 1955; Bayly and Williams, 1966). Thus, samples from different sea-

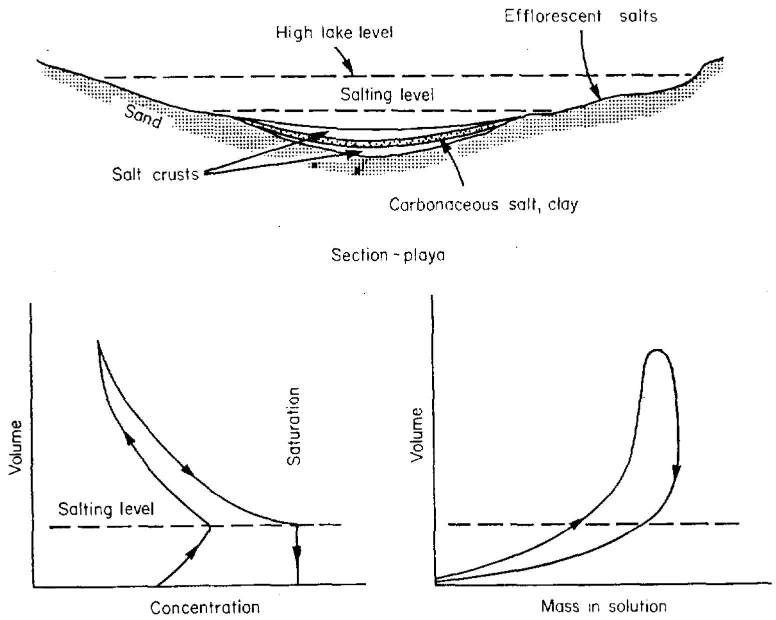

Fig. 5. Salt regime of a playa lake. Modified from Langbein (1961).

sons vary far more in concentration than in composition. The ionic composition of the lakes within a region may be quite varied, however, and data from different lakes best demonstrate sequential change in relative ionic composition, as shown in Figs. 6–10. These figures were designed chiefly to portray the composition of waters in lake districts of arid realms and must not be interpreted as showing evaporative sequences except in a very general way.

B. Chemistry of Desert Lake Districts

Many factors contribute to and affect the chemical composition of closed-basin waters. These, obviously, include all the interrelationships of temperature, precipitation, evaporation, basin sediments, nature of influent waters, lithology of the drainage basin, and biotic effects. Moreover, morphometric details of the lake may play a role in determining the nature of its water.

Hutchinson (1957, Figs. 156, 157) graphed trends in anionic compositions of some closed lakes of the American West and of Indian Tibet as the concentration of materials proceeds. These trends are included with other sequences in Figs. 6 and 7 that portray anionic changes beginning with dilute carbonate water. In general, Hutchinson showed that the

Lahontan Basin lakes of Nevada, some California closed lakes, and the waters of Oregon, that lie now in the depression that contained the Quaternary Lake Chewaucan, terminate as chlorocarbonate lakes. These data are incorporated into Fig. 6. The three series conclude near Winnemucca, Pyramid and Big Soda Lake in the Lahontan waters, Big Borax Lake in California, and Abert Lake in Oregon. The pathway seems to lead through a triple-water type, of which Mono Lake, California, is a good example.

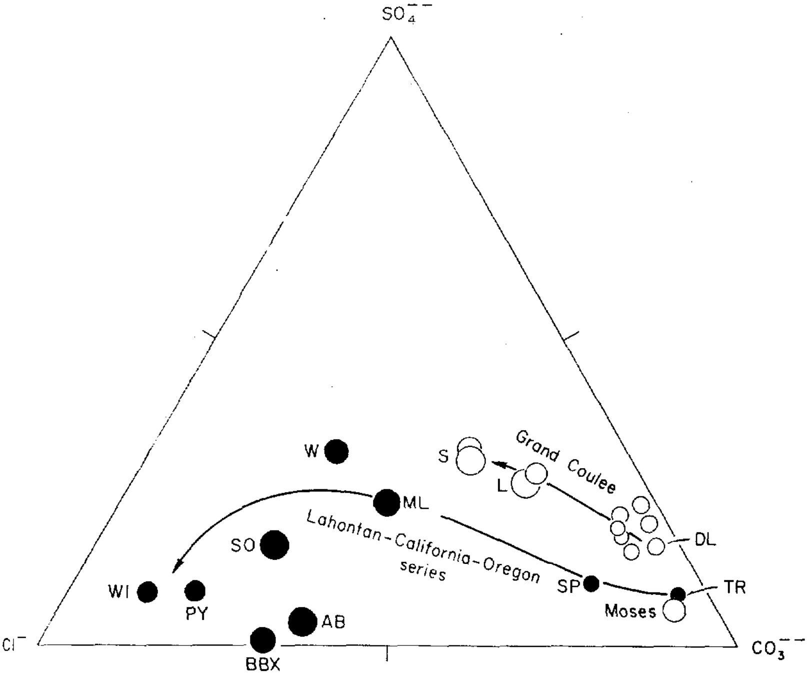

Fig. 6. Triangular coordinate plot of the relative anionic compositions and possible concentration trends of waters of the Lahontan Basin, Nevada, California closed lakes, Chewaucan Basin, Oregon, and the Grand Coulee, Washington. Moses Lake, Washington, included as an example of sodium carbonate waters. Lahontan Basin: TR, Truckee River; W, Walker Lake; SO, Big Soda Lake; PY, Pyramid Lake; WI, Winnemucca Lake. California lakes: ML, Mono Lake; BBX, Big Borax Lake. Oregon waters: SP, spring on shores of Abert Lake; AB, Abert Lake. Grand Coulee Lakes: DL, Deep Lake; L, Lake Lenore; S, Soap Lake. Moses, Moses Lake. Diameter of circles proportional to logarithms of total salinity.

Paralleling these trends to some degree (Fig. 6), but stopping short of the chlorocarbonate category, are the lakes of the Lower Grand Coulee, Washington (Edmondson, 1963). They begin with Deep Lake as it was in 1945 and proceed to Soap Lake, which is near the triple-water category. In this series a high initial content of carbonate compared to chloride, coupled with subequal proportions of calcium and sodium, results in the loss of most of the calcium before the carbonates are significantly depleted. Moses Lake, Washington, although not in this series, goes a step further. Perhaps because of an initially higher calcium content, much of the sulfate is also precipitated in gypsum. This, in addition to the precipitation of mirabilite ($Na_2SO_4 \cdot 10H_2O$) has left Moses Lake water a magnificent example of the sodium bicarbonate type (Fig. 6).

Other series starting with dilute carbonate water, but ending as sulfato-

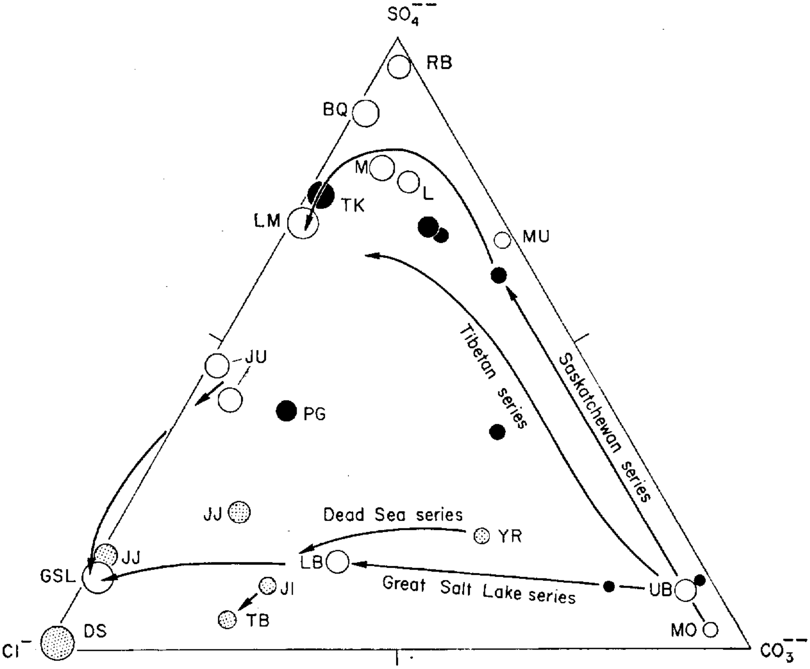

Fig. 7. Relative anionic composition and possible concentration trends of lakes of Indian Tibet (closed circles), closed lakes of Saskatchewan (open circles), Great Salt Lake, Utah, and tributaries (open circles), and Jordan Valley waters (stippled circles). Tibetan lakes: PG, Pang-gong Tso; TK, Tso Kar. Saskatchewan lakes: MO, Montreal Lake; MU, Murray Lake; L, Last Mountain Lake; RB, Redberry Lake; BQ, Big Quill Lake; M, Manito Lake; LM, Little Manitou Lake. Utah waters: UB, Upper Bear River; LB, Lower Bear River; JU, Jordan River, Utah; GSL, Great Salt Lake, Utah. Jordan Valley: YR, Yarmuq River at junction with the Jordan; JI, inlet to Lake Tiberias; TB, Lake Tiberias; JJ, Jordan River at Jericho, two analyses; DS, Dead Sea.

chloride types (Fig. 7), are the Tibetan lakes studied by Hutchinson (1937a) and the saline lakes of Saskatchewan (Rawson and Moore, 1944). The former series terminates near Pang-gong Tso and Tso Kar, and the latter culminates in Little Manitou; the last two lakes contain *Artemia*. The Canadian series, beginning with the carbonate Montreal Lake, includes the unusually fine sulfate waters of Stoney and Redberry lakes, perhaps only surpassed by Hot Lake, Washington, as examples of this type.

The end of the Tibetan and, especially of the Saskatchewan series is a starting point for a cline seen in the Bottomless Lakes, New Mexico (Fig. 8). The most saline of these solution basins is No-Name Lake, a

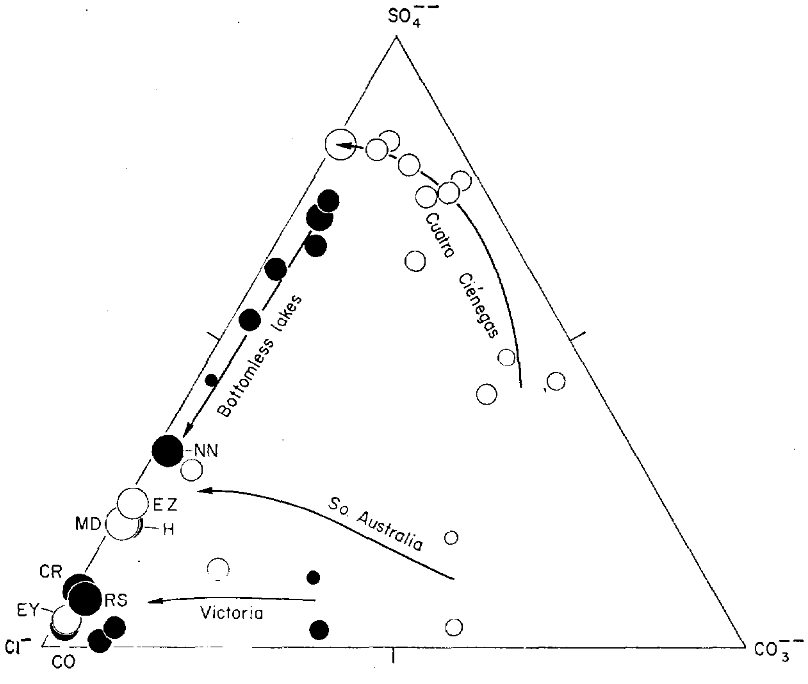

Fig. 8. Relative anionic composition and possible concentration trends in waters of the Bottomless Lakes, New Mexico (closed circles), Cuatro Ciénegas Basin, Mexico (open circles), Victoria, Australia (closed circles), and South Australia (open circles). Bottomless Lakes: NN, No-Name Lake. Victoria: RS, Raah Salt Lake; CR, Lake Crosby; CO, Lake Corangamite. South Australia: EZ, Lake Eliza; H, Hart Lake; MD, Lake Macdonnel; EY, Lake Eyre.

chlorosulfate type. The trend of the plot involves a plunge toward the chloride corner.

The artesian waters of the Cuatro Ciénegas basin in Coahuila, Mexico (Minckley and Cole, 1966) emerge with sulfate and carbonate subequal (Fig. 8). Further concentration leads to the extreme salinity seen in one playa on the boundary of the sulfate and sulfatochloride types. The relative net gain of chloride over sulfate has been slight, and the trend toward chloride water is not so obvious as in the Bottomless Lakes. A continued loss of sulfate is indicated by massive gypsum dunes on the leeward side of one Cuatro Ciénegas laguna; this aeolian loss may nearly balance the input of sulfate via influent rheocrenes. Figure 7 also shows two lakes modified by the large amounts of halide contributed by influent rivers, the Dead Sea and Great Salt Lake, Utah. These were discussed by Hutchinson (1957).

Two series that start with dilute river water are shown in Fig. 9. The first is the Caspian complex, beginning with the influent Volga and ending with the concentrated Gulf of Karabugas, more than 20 times the salinity of the main Caspian. The river waters contain comparatively more sulfate and less carbonate than the streams that feed the closed lakes of western North America (Fig. 6). The pattern accompanying concentration is characterized by a marked loss of carbonate matched by a similar gain in chloride with only a 15% loss in relative sulfate. The Gulf of Karabugas is an important source of gypsum and mirabilite. Its saline waters are at the chlorosulfate and chloride boundary.

The second series in Fig. 9 originates with the Colorado River and ends in the Salton Sea, California, which is much more dilute than the Karabugas. Its ionic composition, although somewhat like seawater, is derived ultimately from Colorado River salts. Evaporation and the dissolving of old deposits have been involved in the concentration. Figure 9 also shows some situations where the initial dilute waters are essentially of the carbonate–chloride or chlorocarbonate type. In these instances sulfate is less than 15% of the three principal anions. The waters of the Long-H Ranch, Arizona (Cole and Whiteside, 1965c), exemplify a good concentration series. There is a shift to the left in the plot as relative carbonate is lost between salinities of 0.4 gm/liter and 2.2 gm/liter. Further concentration to 61 gm/liter shows a precipitous decline in sulfate. After this, additional concentration results in a shift toward chloride water, but low calcium content and a high carbonate level may preclude passing beyond the chlorocarbonate category. Similarly, the soda waters of Lake Rudolf, Africa, if represented in a concentrated state in Crater Lake A, show a slight shift from carbonate–chloride toward the chloride corner (Fig. 9).

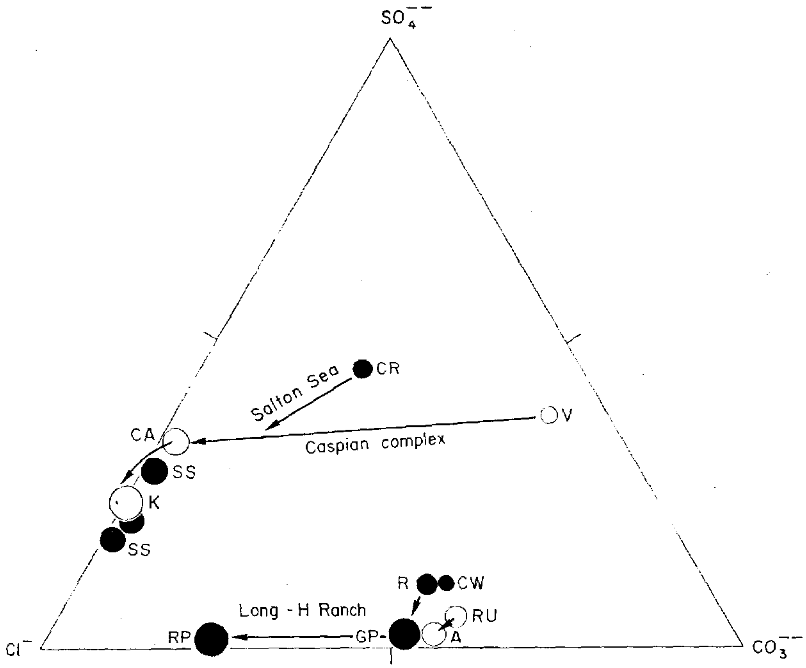

Fig. 9. Relative anionic composition and possible concentration trends in waters of the Caspian Sea, USSR, Salton Sea, California, Long-H Ranch, Arizona, and Lake Rudolf, Africa. Caspian complex: V, Volga River; CA, Caspian Sea; K, Gulf of Karabugas. Salton Sea: CR, Colorado River; SS, Salton Sea, three assays. Long-H Ranch: CW, caved-in well, 1934; R, well at Red Pond, 1964; GP, Green Pond; RP, Red Pond. African series: RU, Lake Rudolf; A, Crater Lake A.

The original Lake Rudolf waters contain less than 5% sulfate (Beadle, 1932).

The dilute lakes of Victoria, Australia, are largely sodium waters with relatively high chloride content, probably cyclic in origin. Williams (1964) has reported the following relative ion abundance: Cl > CO_3 > SO_4 and Na > Mg > Ca > K. The concentration trend (Fig. 8) leads to the chloride lakes Crosby, Corangamite, and Raah Salt. The main changes involve a reversal of the relative positions of carbonate and sulfate and of the cations calcium and potassium.

The South Australian series (Fig. 8) commences with carbonate–chloride water and terminates with chloride waters much like the salt lakes of Victoria. The more nearly normal situation with the calcium level greater than magnesium exists in the dilute lentic waters of South Australia. In spite of this the trend proceeds to the extreme condition shown in Lake Macdonnell, which is a magnesium chloride lake with no calcium (Williams, 1965a). The other saline lakes, Eyre, Eliza, and Hart, are of the sodium chloride type (Fig. 8).

Ruttner-Kolisko (1964) and Löffler (1961b) have furnished data that make possible plotting ionic composition of varied Iranian waters, large and small (Fig. 10). The most dilute water is the carbonate type, but the majority of the waters of no more than 1.0 gm/liter salinity are triple waters. Concentration leads either to sulfatochloride water or to the chloride type as in Lake Urmia. Livingstone (1963) states that most Iranian lakes are highly evolved sodium chloride lakes, and he suspects the presence of halide beds in the vicinity. The rainwater of this region, however, has a high conductance because of salt derived by wind from the Dasht-i-Kavir (Ruttner-Kolisko, 1964), and aeolian salt could be the source.

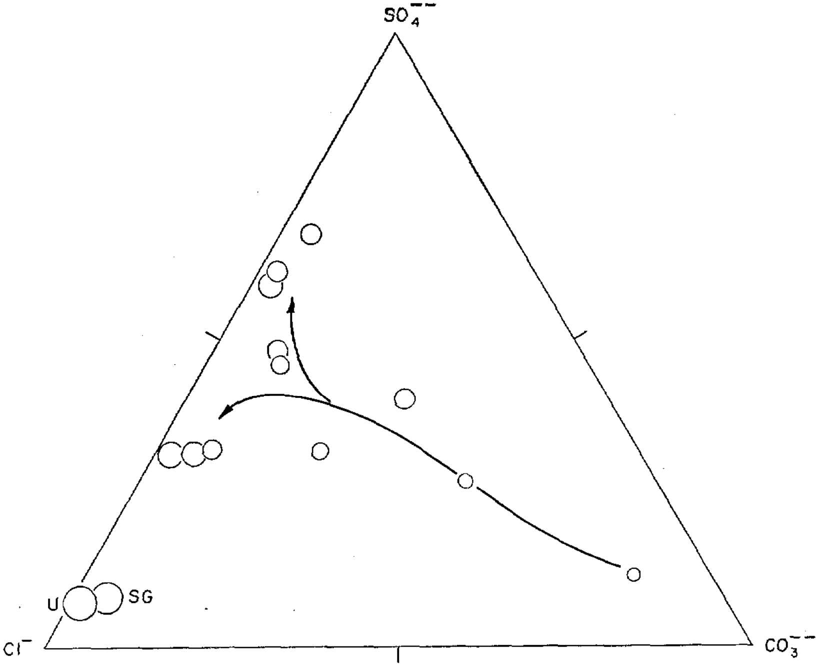

Fig. 10. Relative anionic composition and possible concentration trends in Iranian desert water. U, Lake of Urmia; SG, Schor-göl.

C. Origin and Loss of Salt

The total salinities of closed basins are closely correlated with climatic conditions, especially net evaporation. The concentration of river and runoff water is thus of prime importance. Figures 6–10 show that increasing salinity in closed-basin lakes is accompanied by the relative increase in chlorinity and, furthermore, there is a decreasing variability in the chloride percentage as salinity mounts (Langbein, 1961, Fig. 10). Other factors, including lithology, alter this, and complex interactions exist. The extreme chlorinities of the Great Salt Lake and the Dead Sea can be attributed to the fact that their major influents flow through extensive salt beds. Furthermore, in the case of the Dead Sea, evaporation from the surface of Lake Tiberias, 112 km upstream, may accentuate this; the annual evaporative loss at Tiberias is on the order of 2.7×10^8 m^3.

In the Caspian Sea, with its tremendous wind–effective dimensions and wave action, the loss of salts via aerosols may be greater than any gain by this method, but in some smaller bodies of water, aeolian gain far outweighs the loss. It long has been observed that monsoon winds carry great quantities of salt 650 km from the Rann of Cutch to the Sambhar Salt Lake in northern India. The concentrated lakes of south Texas, La Sal Vieja, and La Sal del Rey may receive their salts by way of the trade winds from evaporated sea water 48 km away (Deevey, 1957). Several proposals have been made to explain the origin of the salt in Australian waters; most authors agree with Anderson (1945) that it is cyclic salt derived from the Pacific in rainwater. Winds from the Dasht-i-Kavir distribute chlorides to many Iranian waters (Ruttner-Kolisko, 1964).

The issue of saline springs or the upward movement of groundwater from buried beds contribute salt to some waters. Lakes of the extensive graben known as the Salt Basin in Trans-Pecos, Texas, owe their salinity to such sources, although subsequent evaporation converts some of them from relatively dilute sulfatochloride waters to chloride brines (Deevey, 1957). Similarly, the playas of the Llano Estacado slightly to the northeast gain their salinities from underlying Permian sediments of marine origin (Meigs *et al.*, 1922). Beadle (1943) attributed the salinities in ponds on the coastal plain, behind and east of Oran, to the leaching of Triassic rocks, with subsequent evaporation playing a small part except at the height of summer.

The differential concentration of certain ions may be brought about in various ways; of these, chloride concentration from sea winds or from old halide beds has been mentioned. The high potassium level in the Nebraska Sandhills lakes may be the result of leaching the ashes of old fires (Hicks, 1920). Sulfate waters are probably derived from the basin soils. In some instances the prior freezing of seawater could have formed extensive beds of mirabilite that go into solution later (Hutchinson, 1957). One of the finest examples of sulfate waters is Hot Lake, Washington, which occupies a basin in epsomite (Anderson, 1958b).

Estimated ages of closed lakes based on the annual salt input in relation to total salinity probably fall short of reality because loss of salt may strike a rough balance with input. Moreover, relatively recent climatic fluctuations may have altered salinity and thus obscured the lake age; a small rise in precipitation and humidity, e.g., may have changed a closed basin to an open one in the past with attendant salt loss and dilution. Factors in the loss of salt from closed basins are discussed below.

Seepage through sandy deposits at the lake margin can account for a nearly continuous salt loss; this seems to occur at the Aral Sea extensively. Groundwater rising at Big Soda Lake during the first quarter of the century moved through the basin, diluting and carrying away great amounts of salt (Hutchinson, 1937b).

The isolation of marginal pools or bays, precipitation of salt, desiccation and the subsequent loss via wind transport may be regular features of astatic desert lakes. Under extreme conditions the entire lake will disappear and deflation will remove immense quantities of the evaporite. Thus, the present low salinity of Walker Lake, Nevada, could be explained as the result of a period in the past when its basin was dry (Hutchinson, 1937b).

Even in the absence of strong wind action, salts can be lost from marginal pools and not be available when flooding next occurs. Hygroscopic salt deposits that become covered with fine-grained material of aeolian origin may not dissolve when reflooded. Similarly, during the first 2 years the Salton Sink was flooded, re-solution of the old salina contributed 79% of the total mass of salt in the Salton Sea, but the rate of solution decreased rapidly in the following years (Arnal, 1961). The decrease in rate can be explained, in part, by the readily soluble salts going into solution immediately, but the deposition of about 0.75 mm of clay sediment per year created a barrier between Salton Sea waters and the less soluble salts that became denied to them as a result. Also, calcitic and dolomitic precipitates represent almost permanent salt loss because they do not go into solution readily.

In large basins there is a mechanism for almost continuous salt loss, if certain morphometric conditions prevail. The Gulf of Karabugas is nearly separated from the main body of the Caspian by two sandy spits (Zenkevitch, 1963). The level of the Caspian is 3 meters above that of this broad shallow bay, and each day 3.2×10^8 kg of salt are carried through the narrow inlet, never to return. Extreme summer evaporation has increased the salinity of the Gulf to more than 20 times that of the main Caspian, and it displays the maximum salinity in the entire complex Caspian system. From 1897 to 1938 the salinity rose from 16.4 to 28.1%, about the limit of saturation; the present mean salinity is said to be about

26.2%. Enormous quantities of mirabilite are precipitated in the deeper parts of the Gulf, and gypsum crystals occur in the shallows; the former is precipitated mainly during the winter months as in other desert waters (Anderson, 1958a; Edmondson, 1963). The salinity of the Caspian Sea has not increased significantly, although some 17.7×10^7 kg of salt are brought in each day and the annual evaporation practically equals the water received from rivers and rainfall. The salt loss through the inlet to the Karabugas may play a considerable role in this balance.

Similarly, at Lake Rudolf, the third largest of the African Rift Valley lakes, a sand spit encloses Ferguson Bay, nearly separating it from the main body (Beadle, 1932). Total alkalinity and phosphorus values in the Bay surpass those from the lake proper, and this probably applies to total salinity.

The recent construction of a stone railroad trestle across Great Salt Lake, Utah, has resulted in a similar situation (Adams, 1964). The northwest part of the lake is isolated, although water can pass through spaces in the trestle and some small culverts, and it functions now as the Caspian's Gulf of Karabugas and Rudolf's Ferguson Bay. Evaporation is great there; as a result, salt-laden water moves through the trestle interstices from the main body of the lake that is becoming increasingly fresh. Much of the salt is precipitated in the northwest basin, but there is some return to the south part of Great Salt Lake. This may be paralleled in the Caspian and Lake Rudolf also. On calm days a density current of saline water runs from the north part of Great Salt Lake beneath the influent water from the south. Following windy weather, seiches of different periods and amplitude arise in the two parts of the lake and waves pass south through the culverts in the railroad fill. Also, during times of high wind, much salt spray is carried south. Wind probably transports some salt from the Gulf of Karabugas back to the Caspian. Certainly, the aeolian loss of salt from the main body of the Caspian Sea is great, and the role of wind transport in the salt balance is significant. Some 5.7×10^7 kg per day are carried by wind beyond the limits of the sea, and this amounts to 30% of the daily amount received via influent streams (Zenkevitch, 1963).

D. Additional Chemical Factors

A few other chemical properties of desert lakes present unusual features when compared to those of lakes in exorheic regions.

Dissolved oxygen is difficult to assay by the Winkler method in many saline waters. In samples from lakes with high carbonate content, the addition of concentrated acid brings about a violent reaction no matter how carefully it is introduced. Soap Lake, Washington (Anderson, 1958a), the Long-H salt ponds, Arizona (Cole and Whiteside, 1965c), and Mono Lake, California (R. J. Brown, 1965) are troublesome waters in this respect. Perhaps inferences concerning dissolved oxygen can be made from the hemoglobin content of *Artemia* in two of these locations. The brine shrimp of the Long-H ponds are intensely red, suggesting a low level of dissolved oxygen (Gilchrist, 1954); conversely, in Mono Lake *Artemia* is white.

In shallow, highly illuminated, saline ponds a benthic or *aufwuchs* flora may produce great amounts of photosynthetic oxygen. An anomalous situation in diurnal samples from such waters in Algeria was described by Beadle (1943). The lower levels simultaneously contained hydrogen sulfide from the reduction of sapropelic mud and also oxygen from bottom-dwelling diatoms.

In meromictic desert lakes there is, of course, a clinograde oxygen curve because of the perennially stagnant monimolimnion. In many of these, the oxygen deficit gives a false impression of high productivity (Hutchinson, 1957). In meromictic Soap Lake, Washington, however, the productivity is unusually high (Edmondson, 1963; Lauer, 1963) and the oxygen deficit may not be so anomalous.

As a result of abundant sulfate resources and extended periods of monimolimnetic anaerobiosis, the deeps of desert meromictic lakes contain tremendous amounts of hydrogen sulfide. Outstanding examples are Big Soda Lake, Nevada, with 786 mg/liter (Hutchinson, 1937b), and Soap Lake, with more than 6000 mg/liter total sulfide (Edmondson, 1963).

Hydrogen ion concentration is relatively stable in well-buffered, concentrated, saline waters. In closed basins containing soda waters the pH is extraordinarily high; pH values of 10 are common, and in the closed, alkaline Lake Nakuru of Africa, a value of 12 has been reported (Jenkin, 1932). In the hard-carbonate limnocrene, Montezuma Well, Arizona, with a mean total alkalinity of 560 mg/liter and no residual acidity, the pH ranges from 6.15 to 6.9, implying free CO_2 in amounts up to more than 600 mg/liter. This may explain the absence of fish (Doudoroff, 1957).

The lakes of arid regions, in general, have higher silica contents than do the waters of humid temperate regions, but not necessarily more than those of humid tropical regions (Hutchinson, 1957, Table 112). In some cold desert regions the erosion of volcanic deposits contributes silica, and silica-rich thermal springs are common in many arid zones. A series given by Whitehead and Feth (1961) shows, however, that the silica of closed basins in the western United States is lower in concentrated waters than in those diluted by influents or in nearby open lakes. There is also an apparent decrease in silica with increasing alkalinity in the central African lakes (Beadle, 1932). In the west Texas waters analyzed by Deevey (1957), the three most concentrated waters had the lowest silica content. Silica rarely can be demonstrated in the concentrated (10–22%) Long-H salt ponds (Cole *et al.,* 1967).

Phosphorus in turbid desert waters is characterized by an unusually high seston fraction (Deevey, 1957); this is discussed with productivity in Section IV,E. The highest known total phosphorus contents are from saline closed basins of arid climates (Hutchinson, 1937b, 1957; Anderson, 1958a). Owens Lake, California, with a reported 78 gm/meter^3 and Goodenough Lake, British Columbia, with 208 gm/meter^3 were mentioned by Hutchinson (1957). In the waters of one pond at the Long-H Ranch, Arizona, inorganic phosphorus ranges up to 150 gm/meter^3 (Cole *et al.,* 1967). There is some evidence that decay following the crash of *Artemia* populations contributes much of this.

The abundance of desert legumes furnishes a unique source of nitrogen in arid–land waters. Fixation by *Acacia* in Australia (Murray and Siebert, 1962) and the mesquite *Prosopis* in the American Southwest seem to be important. Groundwaters near Phoenix, Arizona, contain up to 83 mg/liter of nitrate, but this may be from contamination by commercial fertilizers rather than the desert flora (Hem, 1959).

Boron occurs in enormous quantities in some desert waters. Borax Lake, California, has been reported to contain 850 mg/liter, and Little Borax Lake and Mono Lake have more than 300 mg/liter (Wetzel, 1964).

Fluoride content varies a great deal in natural waters, but high values have been found in desert sources. Hem (1959) reported 32 mg/liter from a well in San Simon, Arizona; in the summer of 1963, when the nearby Willcox Playa held water, it contained 72 mg/liter fluoride. In Quitobaquito Spring, south-central Arizona, 4.3–5.3 mg/liter occurred (Cole and Whiteside, 1965a).

IV. Productivity

The lakes of arid Indian Tibet show greater hypolimnion oxygen deficits than those with similar surface temperatures in the high mountains of Europe (Hutchinson, 1937a). The Tibetan Lakes are mesotrophic; their European counterparts are oligotrophic. Hutchinson proposed that the difference is brought about by the arid climate, with intense solar radiation and the concentration of nutrients being especially important factors. Most other reports from arid regions imply relatively high productivity in desert waters.

Pyramid Lake, Nevada, is morphometrically oligotrophic, with a summer oxygen profile suggesting low productivity. The hypolimnetic areal oxygen deficit, however, amounts to 0.09 mg O_2/cm^2/day (Hutchinson, 1937b), which is high in the eutrophic range. This rate of oxygen disappearance may be invalidated as an index of productivity by the decomposition of aeolian allochthonous material, however.

A. Primary Productivity

Published studies on aquatic primary production in deserts are infrequent, and it is difficult to assess and compare results because of the diverse methods employed and the various ways data are presented. Beadle (1932) calculated the amount of CO_2 assimilated at four stations in Lake Rudolf between dawn and noon. Data were obtained from titration of samples to phenolphthalein and methyl-orange end points with standard acid. His stations can be arranged in a series of increasing total alkalinity from the open water of the lake proper, through Ferguson's Gulf to two shallow beach pools. The computed CO_2 turnover rates increased accordingly; the intensity of the supposed photosynthesis in the open lake was one fifth that of the most concentrated pool in which a tremendous population of *Arthrospira* flourished. Beadle's data are not expressed on an areal basis, precluding most comparisons, but the half-day change in the most alkaline water would amount to the fixation of more than 28 ml CO_2/liter! Undoubtedly, carbonate deposition accompanying photosynthesis is reflected in the computations and obscures the actual productivity rate.

The mean annual gross photosynthesis in Peña Blanca Lake, Arizona, was estimated at 1.6 kg O_2/m^2 (McConnell, 1963). About 50% of this was derived from benthic plants. During 1964 Kemmerer (1965) found slightly higher productivity. He expressed the results on a volumetric basis, estimating 292 gm O_2/meter^3; McConnell's pelagial productivity expressed similarly would be 249 gm O_2/meter^3.

Unpublished data from Montezuma Well, a limnocrene in the Verde Valley of Arizona, show high primary productivity. Monthly means during 1960–1962 imply a mean annual production of 2.55 kg O_2/meter^2. On a volumetric basis this amounts to about 382 gm O_2/meter^3 in the photic zone. Montezuma Well's continuously growing *Potamogeton* community represents a standing crop of at least 800 gm dry weight/meter^2, and this is comparable to the highest figure for aquatic macrophytes presented by Westlake (1963).

The impoundment at Quitobaquito Spring, Arizona (Cole, 1963), disclosed a gross primary productivity of 3.3 gm O_2/meter^2/day in late May (Cole and Whiteside, 1965a). Submersed benthic plants contribute much to the productivity in this shallow pool, which is almost uniformly 1 meter deep.

Wetzel (1964) used ^{14}C methodology to calculate an annual mean fixation of 1060 mg C/meter^2/day in the shallow Borax Lake, California. Assuming a PQ of 1.25, this amounts to a net productivity of 1.3 kg O_2/meter^2/year. Almost 70% of this was derived from the periphyton, emphasizing the relative importance of littoral productivity in very shallow lakes. Periphyton production rates were studied in another way by Castenholz (1960), who measured the increment of organic material on glass plates. He compared rates of production in two of the dilute freshwater lakes of the Grand Coulee chain with the saline Lake Lenore and Soap Lake. The maximum daily rate observed was 1043 mg/meter^2 in Soap Lake.

In the upper meter of the Salton Sea, the net primary productivity amounts to a daily mean of 2.0 gm O_2/meter^2, and the dry weight of plant material produced is estimated at 6.2×10^3 kg/ha/annum (Carpelan, 1961). In the Alviso salterns the mean daily productivity is equivalent to the fixation of 3.9 gm C/meter^2 (Carpelan, 1957).

Richardson (1964) reported a daily gross primary productivity of 7.15 gm O_2/meter^2 in Lake Naivasha, lying in the semiarid portion of the Eastern Rift Valley of Kenya. Perhaps an annual gross production on the order of 2.0 kg O_2/meter^2 can be inferred from this.

The planktonic algal populations, developing during the brief periods that the White Nile near Khartoum is impounded, fix 2.2 gm C/meter^2/day (Prowse and Talling, 1958). On an annual basis this would approximate 2.6 kg O_2/meter^2.

Lake Tiberias, in the Jordan Valley, is essentially a freshwater lake, oligohaline at the most. Samples from a bay of the lake show that from October to January respiration seems to exceed oxygen production and photosynthesis is greatest during February and March. In March, daily gross productivity amounts to 3–4 gm O_2/meter^2 (Yashouv and Alhunis, 1961).

These data from scattered sources show primary productivity in desert waters is comparable, on an areal basis, to that of most eutrophic lakes. If lacustrine trophic status is more closely related to a volumetric expression of productivity, many desert waters are far more productive than most eutrophic lakes of temperate regions. For example, the maximum depth of the productive Borax Lake is rarely as great as 1 meter (Wetzel, 1964).

B. PLANKTON

Under conditions of aridity, as salinity mounts in desert waters, their plankton populations are increasingly impoverished in species; on the other hand, total numbers and mass may become great. The portrayal of zooplankton densities in Soap Lake and Lake Lenore (Edmondson, 1963, Fig. 13.6) shows this clearly. Vertical hauls from eleven of the Saskatchewan lakes implied a mean of 121 kg/ha dry weight of plankton (Rawson and Moore, 1944); the six most saline lakes had a mean of 174 kg/ha—the mean of the five others was 56 kg/ha. Thus, the six saline lakes are comparable to the rich Lake Mendota, Wisconsin (see Northcote and Larkin, 1963, Fig. 16.6).

The minimum phytoplankton productivity of the Salton Sea may be greater than any reported from the oceans during upwelling (Carpelan, in Arnal, 1961). The maximum bloom is vernal and is followed by a peak in the consumer foraminiferans in late spring and early summer.

The data on algal standing crops from the Alviso salterns, California (Carpelan, 1957), may be complicated by factors other than salinity. For example, the mean standing crop of *Stichococcus bacillaris* in the sixth pond of the evaporative series is 1.6 times greater than in the more dilute third pond. However, *Artemia* is the main consumer in the sixth while marine copepods occur in the less condensed ponds of the series; *Stichococcus* passes through the gut of *Artemia* unharmed (Gibor, 1956).

Carpelan (1957) estimated eight generations per annum of *Artemia* in the briny sixth pond of the Alviso salterns and an annual dry-weight productivity of 62.6 kg/ha. This represents high productivity when the shallowness of the pool is kept in mind. *Dunaliella salina* is probably the main food item of this primary consumer; Mason (1963) showed that an adult brine shrimp may devour 6.4×10^6 cells daily.

C. BENTHOS

The benthic standing crops of arid–region lake districts are probably more variable than those of other districts. The astatic nature of desert waters may preclude the development of a bottom macrofauna in many instances. In more nearly permanent lakes, however, enormous faunas composed of relatively few salt-tolerant species develop. This was predicted by Deevey (1957) after he examined benthic samples from some shallow, West Texas waters.

A list of the seven richest lakes in North America with respect to standing crop of benthos includes four from arid or semiarid regions (Cole and Underhill, 1965). The wet weight of bottom fauna from Last Mountain Lake and Echo Lake, Saskatchewan, amounts to 573 and 387 kg/ha, respectively. The former may be the richest lake on the continent in this category. The reason for the outstanding benthic crops in these lakes, when compared with others that were intensely dredged and studied by Rawson and Moore (1944), may be a function of the relative abundance of cations rather than of total salinity. In Last Mountain and Echo there is a pronounced excess of sodium over magnesium; this is not true for the others. Temperature, turbidity, and morphometry were ruled out as the factors setting these two productive lakes apart from the others.

The other North American productive lakes from arid regions are Soap Lake and Lake Lenore, Washington. Their mean wet weights of benthos are 297 and 288 kg/ha, respectively (Lauer, 1963). These figures are minimal because their abundant beetle and corixid faunas cannot be sampled adequately on a quantitative basis.

D. FISH PRODUCTION

Estimates of fish production in desert regions range from low to extraordinarily high. In the open Lake Tiberias annual production is only 57 kg/ha, but in nearby fish ponds, 3000–4000 kg/ha are produced with artificial feeding (Yashouv, 1961). In the comparatively new Arizona impoundment, Peña Blanca, the fish harvested by anglers amount to 155 kg/ha/annum (McConnell, 1963). Wurtz and Simpson (1964) estimate the soda waters of Lake Rudolf may produce 300 kg/ha/annum.

In southern Israel, acclimatization of *Tilapia* and *Mugil* to high salinities has resulted in increased productivity (Fishelson, 1965). *Tilapia,* usually raised in ponds of 300–350 mg/liter chlorinity, has been acclimatized to 1.5–4.0 gm/liter with a 25–35% higher yield resulting. Two saline ponds, totaling 1.5 ha, produced 1965 kg of the two species in 300 days without artificial feeding.

E. ANEMOTROPHY

Some reports demonstrating clearly the effect of zooplankton grazing on phytoplankton populations are from desert lakes (Anderson *et al.,* 1955; Anderson, 1958a; Wetzel, 1964). The nutrition of arid–land waters at the lower trophic levels is not always so ideal as this, however. In many instances chlorophyllous producers do not occur or are very sparse. This is particularly true of extremely turbid ponds, both ephemeral and permanent. Hutchinson *et al.* (1932) designated turbid pools of the Transvaal as Blaauwater Pans and suggested their primary source of nutrition was organic matter in the suspended particles that imparted the turbidity. Hutchinson (1937b) noted teeming entomostracan populations in the turbid waters of Big Washoe Lake, Nevada, and presented evidence that the crustaceans were feeding on bacteria supported by allochthonous material of aeolian origin. He suggested anemotrophy may be widespread in arid, windswept regions, the particles driven to shallow basins forming the basis of an argillotrophic food web; in deeper lakes eutrophy would be furthered by the arrival of aeolian material.

Very little is known about suspended particles, but Deevey (1957) found about 85% of the total phosphorus in the playas of West Texas was adsorbed or bound to the seston. In turbid ponds of the Sonoran desert of Arizona, especially in those of a temporary nature, there is a high sestonic phosphorus fraction when compared to volcanic lakes on the Colorado Plateau. In many of those desert ephemeral ponds the sestonic phosphorus is over 90% of the total; in the volcanic lakes around Flagstaff there is high turbidity derived from volcanic-ash sediments, but the mean sestonic phosphorus is only about 25% (Cole, 1966b). In Little Triste Pond near Chandler, Arizona, there is a dense cladoceran and diaptomid population, but usually algae are absent or are very scarce (Barry, 1965). Secchi-disc values are as low as 2–3 cm, and often the algae are limited to a surface scum. It is extremely difficult to demonstrate chlorophyll in water samples from Little Triste because membrane filtration permits only 10 or 15 ml of water to pass before complete clogging. This applies to most turbid ponds of the Arizona desert.

V. Biota of Saline Water

Many researches on the physiological and ecological aspects of saline desert waters have been summarized recently by Macan (1963). Hedgpeth (1959) preceded him with schemes for classifying saline habitats and with long lists of organisms that have been reported from waters more concentrated than those of the sea. The present discussion of necessity is abbreviated, but it is not intended to be a condensation of the two excellent works mentioned above, nor should it preclude consulting them.

Bayly's (1967) biological classification of the Australian aquatic environments contains much pertinent material and questions the applicability of older categories. It is his opinion that marine and inland saline waters lie at opposite ends of a biological spectrum of aquatic habitats. Thus, the continental Australian centropagid copepods have marine forerunners that successively occupied brackish, fresh, and inland hypersaline water. The species characteristic of the highest salinities seem to have had immediate freshwater ancestors.

A. FLORA

In general, the diversity of algal species is inversely correlated with salinity and in most instances blue-green algae and diatoms persist in concentrated waters where chlorophyceans are rare. Thermal waters, common in arid regions, also are characterized by blue-green algae and diatoms.

Kuehne (1941) reported 292 phytoplankters from the saline lakes of Saskatchewan. Only 13 or 14 species were in Little Manitou, of 12% salinity. Manito, Little and Big Quill lakes with salinities of 2–3%, had 42 species. The poor representation of green algae in the more saline Canadian lakes is also the case in Devils Lake, North Dakota (Moore, 1917; Moore and Carter, 1923), which shows close floral affinities to the former.

Beadle (1932) traced a concentration series in the soda waters of high pH value at Lake Rudolf. This started with the open lake, progressed to the more concentrated water of Ferguson's Gulf, and culminated in beach pools and some insular crater lakes. From this a rough arrangement of algal genera, in order of increasing tolerance to concentration, can be made: *Botryococcus, Hormidium, Phormidium, Anabaenopsis,* and *Arthrospira.*

The impoverished flora of the Caspian's saline Gulf of Karabugas includes hardly more than the cyanophyte *Aphanothece salina* and two species of the green flagellate *Dunaliella* (Zenkevitch, 1963).

Flowers (1934) reported three blue-green algae and two chlorophyceans from the open water of Great Salt Lake, Utah. Further data summarized by Bradley (1963) include 13 algal species, 12 bacteria and 62 diatoms, although these are not all planktonic. In the more dilute springs and pools near the shore a few species of filamentous green algae, *Chara contraria* and *Enteromorpha* occur (Flowers, 1934). In hot springs around the lake there are at least 18 species of blue-greens. The occurrence of certain blue-green algae in hot springs seems to be universal, but an exception to the generalization was noted with interest by Beadle (1943); in the Fontaine Chaud near Oran, *Spirogyra* occurred and Cyanophyta were absent.

Six species of diatoms were found to be limited to the more saline lakes of the Saskatchewan series (Kuehne, 1941; Rawson and Moore, 1944). These included *Chaetoceros elmorei,* a rare representative of a marine genus that has been reported from Devils Lake, North Dakota, and the Grand Coulee lakes, Soap and Lenore (Anderson, 1958a; Edmondson, 1963). This leads to an examination of the occurrence of this marine genus in the flora of inland saline waters. Beadle (1943) listed a *Chaetoceros* from Algeria, but showed that it occurred in waters below the density of seawater and did not range into extreme salinities where other diatoms occurred. Anderson (1958a) pointed out that *Chaetoceros* was absent from Soap Lake in 1950 when its salinity was 3.5% but appeared in bloom porportions during 1954 when the salinity was only 2.8%. Other data suggest that 3% salinity may be about the upper limit for this genus. It flourished in Devils Lake at 1.3% (Young, 1924) and in Lake Lenore at 1.4% (Anderson, 1958a). In the Saskatchewan lakes it was especially abundant from 1–3% salinity but also occurred in dilute waters of 0.04% (Rawson and Moore, 1944).

Similar things may be said for the marine genus *Enteromorpha.* In Algeria its distribution in relation to salinity was similar to that of *Chaetoceros* (Beadle, 1943). It occurs in dilute situations along the shores of Great Salt Lake (Flowers, 1934), in Devils Lake in salinities of about 1% (Moore, 1917), and is in the low salinities of Arizona irrigation canals (Wien, 1958). In the Alviso Salt Ponds, California, where water in a series of evaporating pools ranges from seawater to a sodium chloride saturated condition, it occurs only in the more dilute ponds (Carpelan, 1957). It occurs in freshwater drainages that enter the Salton Sea but is absent from the saline main body (Carpelan, 1961). Most algae of hypersaline situations appear to have a freshwater ancestry rather than a recent marine origin. Perhaps most marine species do not tolerate water that is osmotically much different from seawater.

In Arizona, the halophyte *Najas marina* occurs in oligohaline waters, but is absent from saline ponds of 11–22% salinity (Cole, 1963, p. 419, Cole and Whiteside, 1965a). Marginal emergent macrophytes show marked zonation based on salinity gradients (Bolen, 1964; Cole and Whiteside, 1965c).

One green alga that is remarkably tolerant to high salinities and is probably restricted to them is the rare *Ctenocladus circinnatus.* Reports of its occurrence in North America are few: a saline beach pool in California (Smith, 1933, p. 418); Little Manitou Lake, Saskatchewan (Kuehne, 1941); Borax Lake, California (Wetzel, 1964); and the twin salt ponds at the Long-H Ranch, Arizona (Cole and Whiteside, 1965c). These sites represent markedly different ionic composition; they include chloride, sulfate, and carbonate waters.

The green flagellate *Dunaliella* is perhaps the most noteworthy chlorophycean with respect to salt tolerance. It "blooms" profusely as mirabilite precipitates in the Gulf of Karabugas and in the Alviso Salt Ponds it becomes the dominant alga after calcium sulfate precipitates and blooms in water saturated with sodium chloride (Carpelan, 1957). Some reports of *Chlamydomonas* in extremely saline situations may be referable to *Dunaliella*.

B. Invertebrate Fauna

Some invertebrate animals are common to inland saline waters throughout most of the world. Others are represented in different regions by closely related species or ecological equivalents. The rotifers *Brachionus plicatilis* and *Hexarthra fennica* are widespread, as is the brine shrimp *Artemia salina*. *Daphnia similis* is holarctic in fresh to moderately saline waters and even occurs rarely at 12% salinities (Rawson and Moore, 1944; Brooks, 1957). The ostracod *Cyprinotus salinus* also may be distributed widely in southern holarctic regions in salinities up to 2.5% (Löffler, 1961a,b). *Nitocra lacustris*, an harpacticoid copepod, occurs in saline waters as widely separated geographically as Iran and Mexico. Similarly, *Onychocamptus mohammed* occurs in salines of four continents.

The North American cladoceran *Moina hutchinsoni* may represent the ecological equivalent of the Old World's *M. salinarum*. Several species of *Moina* have been collected from saline water (Löffler, 1961b), and they also occur in polluted situations. *Diaptomus nevadensis* of western North America may be restricted to saline waters (Wilson, 1958) and is comparable to *D. salinus* of Europe and North Africa. The harpacticoid genus *Cletocamptus* includes several saline-water species and in North America is represented by *C. albuquerquensis*, ranging at least from the most saline Saskatchewan lakes (Rawson and Moore, 1944) to a playa in Coahuila, Mexico, with total dissolved solids of 309 gm/liter (Minckley and Cole, 1966). Many cyclopoid copepods occur in salines; several of these are distributed widely and, in addition, there are regional representatives involving different species in different parts of the world. The phyllopod genera *Branchinella, Branchinectella,* and *Branchinecta* include species found at higher salinities than most anostracans, with the exception of *Artemia*. In North America, *Branchinecta campestris, B. lindahli,* and *B. mackini* are probably the most euryhaline. The first two sometimes coexist with *Artemia* (Lynch, 1960, 1964).

Perhaps the most remarkable crustaceans of inland hypersaline waters are the Australian isopods referable to *Haloniscus*. The genus belongs to the Oniscidae, a family including mostly terrestrial species. The occurrence of Isopoda in concentrated waters is unknown outside of Australia (Williams, 1965b).

Among the insects, the Diptera, especially, include hardy species.

Ephydrids are well-known occupants of strongly saline water, and the culicid *Aedes detritus* is remarkable for its power of osmotic regulation (Beadle, 1939). The larvae of the ceratopogonid *Culicoides variipennis sonorensis* are abundant in water of at least 22% salinity, and even tabanids occur sparingly in such situations (Cole and Whiteside, 1965c). Several chironomids occur in moderately saline water (Beadle, 1943, Fig. 2; Deevey, 1957; Lauer, 1963). Even *Chironomus plumosus* is capable of hypo-osmotic and hyperosmotic regulation and theoretically can live in 1.4% salinity (Lauer, 1963). Rawson and Moore (1944) found it at 1.3% salinity in Saskatchewan.

Many corixids tolerate high concentrations of salt—in the United States, e.g., *Trichocorixa reticulata* and *T. verticalis* occur exclusively in saline waters and have been reported from the Alviso salterns (Carpelan, 1957), the Salton Sea (Barlow, 1958), and Big Soda Lake (Hutchinson, 1937b). Also, *Corisella decolor* and *C. inscripta* are remarkably tolerant to salinity and organic pollution; they occur in the alkaline Little Borax Lake, California (Usinger, 1956). The coleopterans include a few hardy species; one of these, *Hygrotus masculinus,* may be limited to saline waters (Lauer, 1963). Odonatans are usually absent from saline lakes, but the naiad of the damselfly *Enallagma clausum* is capable of osmoregulation and occurs in the most saline of the Grand Coulee lakes (Lauer, 1963) and Big Soda Lake (Hutchinson, 1937b).

In most instances the invertebrates found in the highest salinities are euryhaline, occurring through a wide range of salinities. Those which occur occasionally in estuarine environments (e.g., *Aedes,* some chironomids and corixids, *Brachionus plicatilis*) and those with marked osmotic powers, such as *Artemia,* are not derived from marine ancestors. Perhaps exceptions to this are the harpacticoids of continental waters, *Onychocamptus* and *Cletocamptus,* e.g., that belong to marine families (Wilson and Yeatman, 1959) and the centropagid copepod *Calamoecia* in Australia (Bayly, 1964). Moreover, as seems to apply to the plants, invertebrates from the sea that are found in inland waters are not necessarily capable of marked osmoregulation. For example, foraminiferans and *Palaemonetes varians* are marine forms that occur rarely inland in North Africa but are not present in water of much different salinity from the sea (Beadle, 1943).

Bayly (1967) emphasizes a point that suggests the usual reason advanced to explain the absence of euryhaline species (e.g., *Artemia*) in the sea may be too simple. Certainly there are many successful marine species that appear equally vulnerable to predation and it is not predation alone that bars many of the salt-tolerant inland species from the sea. We have tended to concentrate on high salinity and adaptations to it, overlooking, momentarily, the other features of desert aquatic habitats—their gross instabilities and their impermanence. The communities of these habitats include species with marked adaptations to environmental fluctuations that are singularly inadaptive to the stable marine environment. Dahl (1956) stated, "[they] pay for their tolerance to various environmental variations by a reduced power of competition in stable habitats."

Several authors have presented data showing floral and faunal changes that occur as salinities decrease or increase (e.g., Beadle, 1943; Carpelan, 1957, 1958; Anderson, 1958a; Whittaker and Fairbanks, 1958; Löffler, 1961b; Ruttner-Kolisko, 1964). In many cases, interpretation is complicated because of factors other than salinity. The remarkable decline of *Pelopia* and *Cricotopus* in the bottom fauna of Lake Lenore (Lauer, 1963) as salinity decreased from 0.6% in 1957 to 0.23% in 1962, may well have involved predation, competition, or changes in food resources. The usual occurrence of *Artemia* in hypersaline environments is not just a function of osmotic requirements but is probably related to the absence of predators in such habitats. The report by Gauthier (1928) of *Artemia* in water less dense than seawater is remarkable, but not from a physiological standpoint. Certain generalizations apply, however. Increase in salinity of inland waters is accompanied by a decrease in taxa or vice versa. Löffler (1961b, Table 2 and Fig. 10) assembled many data on the salt tolerance of entomostracans from five continents. He listed 183 taxa, of which fewer than 15% occur in waters of 3% or greater salinities. The macrobenthic species of Lake Lenore numbered 19 in 1957, but at least 32 were present in 1962 after dilution had occurred (Lauer, 1963). Concurrently, the number of planktonic species increased (Anderson, 1958a; Edmondson, 1963). The number of taxa in various communities of the saline Saskatchewan lakes decreases from lake to lake as salinity mounts (Rawson and Moore, 1944). In various waters of the arid Columbia Basin, high salinity excludes planktonic species of copepods and results in single-species communities of other crustaceans made up of *Moina hutchinsoni* first and, in more intensely saline waters, *Artemia.*

Recently Bayly and Williams (1966) added some Australian species to the relatively meager list of animals known to occur in waters in excess of 10% salinity. The most noteworthy are ostracods referable to the endemic Australian genus *Diacypris,* and two gastropods.

It is probably valid to arrange various species in order of relative tolerance to salinities, but precise limits are difficult to define. *Diaptomus sicilis* appeared in Soap Lake and became established when the salinity fell below 2%, and *Daphnia similis* was first noted in Lake Lenore when salinity decreased to about 0.67%. These figures, however, cannot be reconciled precisely with the data of Rawson and Moore (1944), who found *D. sicilis* in salinities between 2 and 3% and a few *D. similis* in the water of Little Manitou Lake at about 12% salinity. Furthermore, Whittaker and Fairbanks (1958) clearly show that relations to salinity gradients among copepod species are affected by other environmental factors such as seasonal stability or impermanence. Differing relative proportions of major ions also may account for discrepancies if one considers total-salinity threshholds for a single species in different waters. Recently, the Australian copepod *Boeckella triarticulata* was discovered in alkaline bicarbonate waters at salinities more than twice those recorded previously for this species in waters dominated by chloride (Bayly and Williams, 1966).

Among salt-tolerant organisms there may be at least two distinct physiological groups, at least at the extremes. One group, restricted to chloride-sulfate waters, is represented by *Artemia,* according to several authors. The second group includes the natrophils—those restricted to alkali-carbonate waters. Löffler (1961b) suggests that *Diaptomus spinosus* is typical of soda waters; probably *D. sicilis* in North America is this type—an early synonym, *D. natriophilus,* has some significance. A widely distributed example is the rotifer, *Hexarthra fennica.* Species lists for each group have some merit, but generalizations must be accepted with caution. The discussion of *Artemia* habitats by Cole and R. J. Brown (1967) reveals how erroneous some of our ideas have been about this phyllopod, or this complex of forms called *Artemia salina.*

Although the typical *Artemia* habitat is probably a body of water containing sodium chloride there are notable exceptions. Macan (1963) pointed out the occasional presence of brine shrimp in sulfate waters, but he stated that many data from saline lakes in Africa, Asia, and North America included no occurrence of *Artemia* in lakes of the soda type. Cole and Brown (1967) discuss several authors who have concluded that carbonate, or perhaps a high pH value, is lethal to *Artemia* (Baid, 1958; Croghan, 1958; Löffler, 1961b), but they show that the crustacean does occur in waters of high carbonate content and low hydrogen ion concentration.

Figure 11 shows the relative concentrations of the three principal anions in many *Artemia* habitats. All of these are waters of at least 3.1% total salinity. The actual carbonate is very high in the Long-H ponds (Fig. 11, RP, GP), Mono Lake (Fig. 11, ML), and especially in Jesse Lake and Cook Lake (Fig. 11, J, C), which are two excellent examples of several Nebraskan soda waters from which D. B. McCarraher (1965) has collected *Artemia* for several years. Some other examples of brine shrimp in soda waters are not shown in Fig. 11; these include the former Soda Lake, Washington (Whittaker and Fairbanks, 1958), and perhaps

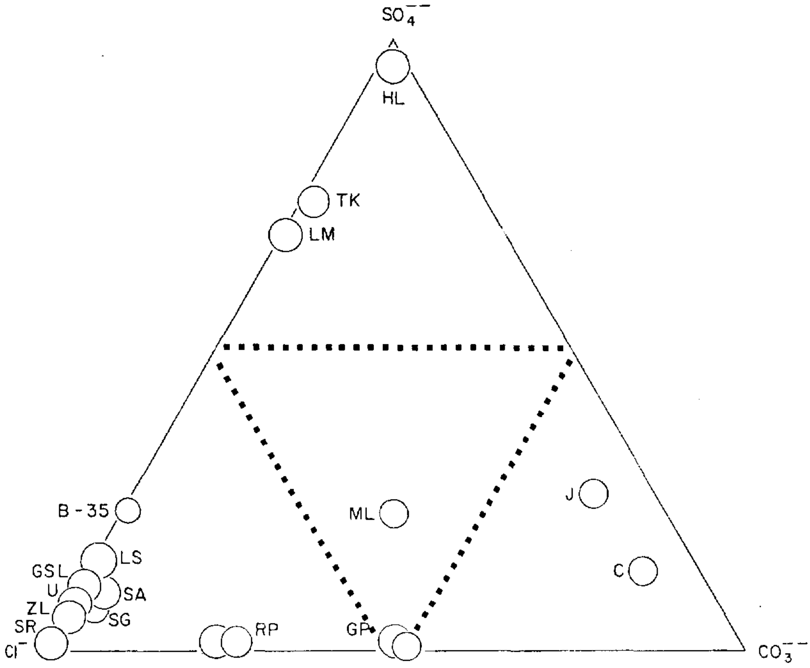

Fig. 11. Relative anionic composition of waters containing *Artemia salina*. Dotted lines are 50% lines. SR, La Sal del Rey, Texas; ZL, Zuñi Salt Lake, New Mexico; U, Lake of Urmia, Iran; SG, Schor-göl, Iran; SA, Sambhar Salt Lake, India; GSL, Great Salt Lake, Utah; LS, Leslie Salt Refining Works, California; B-35, Beadle's Pond 35 (1943), Algeria; LM, Little Manitou, Saskatchewan; TK, Tso Kar, Tibet; HL, Hot Lake, Washington; RP, Red Pond, Long-H Ranch, Arizona; GP, Green Pond, Long-H Ranch, Arizona; ML, Mono Lake, California; J, Jesse Lake Sheridan Co., Nebraska; C, Cook Lake, Sheridan Co., Nebraska. From Cole and R. J. Brown (1967).

Big Soda Lake, Nevada (Fig. 6, SO). During the nineteenth century, *Artemia* occurred in Big Soda Lake (see Hutchinson, 1937b). At that time the carbonate:chloride ratio was greater than in 1933, when *Artemia* was absent (Hutchinson, 1957). The disappearance of brine shrimp may be attributable directly to the freshening that took place as groundwater entered the lake, or indirectly to the arrival of predators and competitors as dilution occurred. The data suggest, however, that it is not high carbonate concentration that precludes survival of *Artemia* in Big Soda Lake.

Several workers have concluded that large amounts of potassium are lethal to *Artemia* unless exceeded substantially by sodium (Martin and Wilbur, 1921; Boone and Baas-Becking, 1931; Croghan, 1958). Cole and Brown (1967) show that there are thriving populations of the brine shrimp in waters where sodium:potassium ratios are very low; most of these are the potash ponds of Garden and Sheridan counties, Nebraska (McCarraher, 1965).

Certain parthenogenetic races have been known for some time that are reproductively isolated from normal bisexual populations of *Artemia* (see Bowen, 1964). Similarly, there is evidence for physiological races that are reproductively isolated by ecological barriers; Bowen reported that the *Artemia* of Mono Lake will not live in a standard culture medium (1 liter seawater plus 50 gm NaCl). Moreover, she found Mono Lake water to be lethal to *Artemia* from Great Salt Lake and the commercial salterns along the California coast. She was unable to develop a compatible medium that would permit crossing the Mono Lake *Artemia* with the others. It is noteworthy that Mono Lake is characterized by an unusually high boron content (Wetzel, 1964) in addition to its carbonate content and high pH.

Morphological distinctions and growth-rate differences are found among populations from different localities (see Gilchrist, 1960; Baid, 1959; Bowen, 1964; Brown, 1965). The salinity of the external medium influences body form and growth, but intrinsic factors play a part in modifying environmental effects. The taxonomy of the animal we call *Artemia salina* is an unsolved riddle.

C. Fish

Euryhalinity is especially well developed in cyprinodont fishes (Beadle, 1943; Barlow, 1958; Kosswig, 1961). Some kinds of desert pup fish (*Cyprinodon*) can withstand concentrations twice that of seawater (Barlow, 1958). In isolated populations salinity seems to induce an increase in meristic characters. The endemic *Cyprinodon salinus* of Salt Creek in Death Valley has more body-circumference scales than related species in less saline waters (Miller, 1943, 1948).

Anomalous development of fish seems to occur in some mineralized waters; this may be a function of ionic composition rather than total salinity. The high incidence of deformity in the introduced *Mugil, Bairdiella,* and *Cynoscion* in the Salton Sea (Walker, 1961) and of abnormalities in the carp of Moses Lake, Washington (Groves, 1951), are notable examples.

VI. Biota of Temporary Waters

A. Lentic Habitats

The environmental features of a temporary pond vary from region to region, but some generalizations can be made. In shallow pools the temperature may be the least conservative factor, following diel air temperatures closely. Dissolved oxygen drops soon after flooding but may fluctuate thereafter. Total electrolytes are low within the first few hours of flooding but rapidly increase and continue to rise in the ensuing days as evaporation reduces pond volume.

Aquatic biologists are prone to assign significance to organisms—some become indicators of permanency, others reveal temporary waters. In humid, exorheic regions this may be valid, but where marked fluctuations in surface level occur during the annual cycle of a pond the classification goes awry. Many astatic ponds that always contain some water, and therefore must be designated permanent, support anostracans, such as *Streptocephalus* and *Thamnocephalus,* and the notostracan *Triops.* The upper expanses of the basin, in these cases, are only temporarily covered by water, and the extreme astacy prohibits the establishment of an ichthyofauna that would eliminate the phyllopods.

Löffler (1961a) pointed out that the shallow waters of arid regions are influenced markedly by climate. This applies especially to temporary pools. The waters of Algeria and Tunisia, studied by Gauthier (1928), lie in three climatic belts based on annual rainfall. Only the ephemeral waters show a differentiation of fauna into three corresponding zones. The permanent waters of the three belts share many species, including several common forms of extensive geographic range. The transitory waters are much richer in species that are, for the most part, interesting for their biogeographical localization. The short-lived rainpools to the southeast in the scrub desert at Khartoum are quite different in faunal aspect (Rzóska, 1961). The relatively long-lived but temporary ponds in Israel along the Mediterranean coast share some species with the *zone steppique* of Gauthier and the Khartoum pools to the south (Yaron, 1964). The faunas of temporary pans in South Africa (Hutchinson *et al.,* 1932) differ notably from those of North Africa and the Sudan. For comparison, however, equivalent species can be substituted from region to region. Thus, *Diaptomus numidicus, D. cyaneus, D. lilljeborgi,* and the large *Hemidiaptomus ingens* occur in the temporary ponds of the Algerian pluvial zone where rainfall is some 50 cm per annum, but *D. chevreuxi* replaces them in the steppic zone where annual precipitation is 30 cm. *D. chevreuxi* is represented by *D. lorteti* in ponds of the more arid desert of North Africa.

The Transvaal pans lie in a region climatically similar to the pluvial zone of North Africa, but some of them are comparable to the r'dirs and dayas of Gauthier's steppic zone. These are the temporary water holes enriched by the faeces of both wild and domesticated animals. *Paradiaptomus transvaalensis* is substituted for *Diaptomus chevreuxi, Daphnia* *gibba* replaces *D. similis* of the north, and several species of phyllopods are replaced by South African counterparts in the Transvaal. An incongruity is the large *Lovenula* in the South African pans. It is best compared to *Hemidiaptomus ingens* in the Algerian pluvial zone, or perhaps to the huge *H. gurneyi* in the Israel pools (Yaron, 1964).

Large calanoids are common in diverse regions where climate is dry for at least part of the year (Hutchinson *et al.*, 1932)—*Hemidiaptomus* species in Asia and Africa, *Boeckella major* in Australia (Bayly, 1964), *D. novemdecimus* in northwestern North America, and the somewhat smaller *D. clavipes* in the American Southwest. The overall picture, however, seems to implicate the annual "climate" of the pool itself, because in humid regions also, the copepod fauna of temporary waters includes unusually large species such as *Diaptomus stagnalis* in Canada and the northern United States. The reason for this may be adaptation for life in an unstable habitat where reestablishment of a population depends largely on survival of resting eggs during dry phases of the pond. This is discussed below.

In parts of North America where aquatic habitats are abundant, certain calanoid copepod species are typical of permanent waters, while others occur principally in ephemeral pools. The latter ponds are usually vernal, clear, and cool. Water is relatively scarce in Arizona, however, and many ponds and lakes go dry at irregular intervals; temporary ponds are especially evident during the summer rains and are turbid and warm. Several calanoid species occur in both fleeting and permanent habitats in Arizona. These are *Diaptomus clavipes, D. albuquerquensis, D. novamexicanus, D. siciloides,* and possibly *D. nudus*. This has presented an opportunity to compare conspecific populations in temporary and permanent waters (Cole, 1966b). The cephalothorax lengths of adults of both sexes are greater in populations from ephemeral ponds than in permanent ponds. This is especially clear in *D. clavipes, D. albuquerquensis,* and *D. siciloides*. Water temperature at the time of collecting is not correlated with size as it is with some copepods (McLaren, 1965). In addition, the clutch sizes are greater in temporary ponds. The number of eggs in a clutch is related directly to female size. Bayly (1962) stated that the number of eggs carried by females of Australian species of *Boeckella* is positively correlated with size and noted (Bayly, 1964) the high mean number of eggs carried by females of *B. major* in a temporary habitat. Røen (1955) reported more eggs carried by *Diaptomus castor* from a Danish temporary pond than from a nearby permanent pond.

The reason for the greater size attained in temporary waters could be a more favorable trophic situation. The fertility that characterizes newly created impoundments is well known; this might apply also to recently flooded desert depressions where detritus of aeolian origin accumulates during dry periods. Furthermore, the "veritable soup of animals" (Rzóska, 1961) that perish a few hours before a desert pool disappears may leave a legacy of nutrients for the next flooding. Also, the trophic structure of turbid, ephemeral waters may be based on argillotrophy, and this could be favorable for entomostracan growth.

Another explanation calls for genetic differences among populations; selection for large size in ephemeral waters may have occurred because of the valuable increase in egg number that follows. Such an idea was proposed by Ravera and Tonolli (1956) for diaptomids compensating for loss of eggs via lake outflow, and Gotto (1962) correlated high egg numbers in parasitic and commensal marine copepods with the hazards of life cycles.

Size differences between temporary-pond and permanent-water calanoids may be emphasized further by predation in the latter habitat. Brooks and Dodson (1965) showed that clupeoid predation seems to eliminate large, freshwater zooplankters and promotes differential survival of smaller species. Such a mechanism could remove the genotypes responsible for large size within a species, bringing about small "races" of *Diaptomus* in permanent ponds.

Gauthier (1928) reported that *Diaptomus* is represented rarely in the permanent waters of North Africa but, by contrast, is abundant in temporary waters where three or four species often coexist. Wilson (1958) wrote that several very large diaptomids in the size range of 3–5 mm often occur together in small, sometimes temporary, pools in the northern prairie regions of North America. Similarly, in Arizona, more species coexist in transitory ponds than in permanent waters and, therefore, similar-sized species occur together more often (Cole, 1966b). There could be two explanations for this. First, an unusually abundant food supply in the temporary waters may permit potential competitors to coexist; this is in agreement with the generalization of Hairston *et al.* (1960) that herbivores may seldom be food limited and are less likely to compete vigorously for common resources than carnivores. A second explanation for the greater numbers of calanoid species in ephemeral waters is the instability of the habitat and the short time for selective pressure to operate.

The adaptations for occupancy of ephemeral waters are varied. Probably dispersal is not so great a problem as withstanding desiccation. Desert dust storms must distribute the resting stages of many species, and birds could serve as effective agents of transport (Maguire, 1959, 1963). Hynes (1955) found six hemipterans in temporary ponds of East Africa; apparently they maintain themselves in permanent waters, flying far and wide across arid lands at the onset of rain. Some traveled from 80 to 100 km to newly formed ponds where breeding may have occurred.

The most striking method of surviving desiccation is the cryptobiosis shown by two chironomid larvae belonging to different subfamilies and occurring on different continents. Hinton (1951, 1960) studied an African species, and Edward (1964) reported an ecological equivalent in Australia. Both species occupy shallow, unshaded, rock pools that are extremely short-lived. The larvae survive as thin, white specks in the dry sediment, becoming active and feeding within an hour after the addition of water. The dry larvae survive experimental temperatures from —270°C to more than 100°C and storage of 10 years at 0% relative humidity.

The sexual eggs of many crustaceans survive long arid periods. The ephippial eggs of *Moina* species and *Daphnia similis* are good examples. Moreover, Gauthier (1928) and Hutchinson *et al.* (1932) remarked on the abundance of male ostracods and on the rarity of parthenogenetic races in arid Africa. The encysted embryos of anostracans are perhaps the best-known examples of resistant stages in temporary ponds.

Among the crustaceans of ephemeral habitats there seem to be at least two kinds of eggs. *Hemidiaptomus ingens* and *Diaptomus cyaneus* probably produce eggs that do not hatch directly (Gauthier, 1928). Delayed hatching occurs also in *D. stagnalis,* an unicyclic inhabitant of temporary pools in humid North America (Brewer, 1964), and there are many other examples. Other species produce both eggs that hatch immediately and those that undergo delayed development and can withstand extended periods of aridity. Probably *D. lilljeborgi* in North Africa (Gauthier, 1928) and *D. clavipes* of the American Southwest are two examples of many such species. *D. siciloides* in permanent lakes of North America produces overwintering eggs that survive in water (Comita, 1964). The fairly common occurrence of *D. siciloides* in Arizona temporary ponds (Cole, 1966b) suggests that these delayed-hatching eggs can also tolerate some desiccation. Among the ostracods there is evidence from Gauthier (1928) that some species produce eggs of only one type, hatching after a period of drying, while other species produce several generations in an ephemeral pond. This probably applies to phyllopods; some conchostracans produce several generations, but *Triops* may be a one-generation species (Rzóska, 1961).

Cyclopoid copepods are not represented by many species in arid-land temporary waters (Gauthier, 1928), although *Cyclops vernalis* and *Eucyclops agilis* appear in some Arizona temporary ponds. In the rain pools near Khartoum, *Metacyclops minutus* survives at least 9 months of the hot Sudanese sun as an encysted copepodid before emerging (Rzóska, 1961). Several cyclopoids undergo resting stages as copepodids (Elgmork, 1955, 1958), but probably few can tolerate desiccation in this fashion.

Because some harpacticoid copepods encyst as morphological adults (Fryer and Smyly, 1954), the occurrence of *Canthocamptus microstaphylinus* and *Cletocamptus retrogressus* in temporary waters (Gauthier, 1928) may imply survival at that stage of development.

There are some cyprinodont fish that produce delayed-hatching eggs that are capable of withstanding desiccation. Not all such species occur in arid lands, but some members of *Nothobranchius* occur in East African regions that fall within the scope of this present chapter (Peters, 1963; Turner, 1964). Their eggs can survive lack of water for several seasons, and it is common to find *Nothobranchius* in ponds that are dry more than 8 months of the year. Within 8–10 weeks after hatching, the fish attain sexual maturity and commence spawning.

Various stimuli have been invoked to explain the hatching of eggs or the emergence of other resting stages, and probably there are more than one. A sudden decline in oxygen that occurs soon after the flooding of a depression may be important to many animals. This is the stimulus that causes hatching in *Diaptomus stagnalis* and *D. caducus* (Brewer, 1964). Also, low oxygen tension at the time of inundation is the final factor triggering hatching of the "eggs" of the fairy shrimp, *Chirocephalopsis bundyi* (Broch, 1965) and of *Aedes* mosquitoes (Horsfall, 1956). Furthermore, this is what breaks diapause in fully developed embryos of the cyprinodont fish of temporary ponds, each species having a particular threshold (Peters, 1963).

The succession of forms that occur during the short existence of a temporary pond reflects, to a great extent, the stages in which they survive aridity. The data of Rzóska (1961) are best for illustrating this succession. Advanced copepodids of *Metacyclops minutus* emerge from their cysts within 10 hours after flooding; by the second day ovigerous females are present, and by the third day many new nauplii have been produced; they become copepodids within 24 hours. *Moina dubia* hatches from ephippial eggs as juveniles that need not undergo metamorphosis; ovigerous females are present the second day; reproduction is parthenogenetic at first, but ephippial females appear within a week. Larval conchostracans appear on the third day, and 48 hours later ovigerous females are present, producing at least one other generation; *Triops* is slower—medium-sized individuals can be collected on the seventh day, and large specimens are present during days 16–20.

Most anostracans probably have a cycle much like that of the conchostracans.

Adult diaptomids appear later than do the cyclopoids (see Yaron, 1964, Fig. 10) because they must pass through more larval stages after emerging. Gauthier (1928) found that unicyclic species of *Diaptomus* disappeared early in a temporary pond's history, while other species with eggs capable of immediate hatching persisted to the end, producing several generations.

In Arizona the final stages of temporary ponds are characterized by arrival of *Ranatra, Notonecta,* and hydrophilid beetles, adding an active predator level to the trophic structure.

In addition to adaptations for surviving desiccation and various other physiological mechanisms whereby life cycles are synchronized with seasonal changes in the pond basin (Broch, 1965), the speed of all biological development is noteworthy. Temperature probably plays a part in this, but genetic differences may be involved also. The species of dragonflies from Australian temporary ponds, e.g., mature much more rapidly than species occupying permanent waters, and experimental high temperatures speed their development (Hodgkin and Watson, 1958). In hot, arid climates, life of the temporary-pond fauna is a race against time, often culminating in the perishing of thousands of animals in the last hours (Rzóska, 1961).

B. Lotic Habitats

Some intermittent stream systems in deserts develop rich faunas of hemipterans, ostracods, and a diverse algal flora. Their fish fauna is sparse, composed of species capable of exploiting the hazardous environment to the utmost. In the vast internal area of the Kalahari Desert, three species of fish persist. These are *Clarias gariepinus,* a clariid catfish equipped with suprabranchial respiratory organs, and two small cichlids, *Tilapia sparrmanni* and *Hemihaplochromis philander* (Jubb, 1965). The three species can survive as stunted individuals in a minimum of water. On the rare occasions that the relict drainage system of the Kalahari floods the desert, these fish, especially *Clarias,* range widely and repopulate suitable habitats. In Arizona, the long-fin dace *Agosia chrysogaster* can survive in the pools of shallow intermittent streams, spreading throughout them at times of flooding (Minckley, 1966). As a result, *Agosia* has persisted in the dwindling waters of the American Southwest, where it is one of the most successful cyprinids (Miller, 1961a).

VII. Special Situations

A. Fish Zonation in Desert Streams and Its Alteration

Man's effect on aquatic habitats in arid regions has been drastic (Miller, 1961a); an overall aspect of this has been a decrease in natural waters and an increase in artificial waters. One of the most lamentable modifications involves an aquatic habitat in which a remarkable fish zonation occurs. The zonation seems to have parallels in several of the world's deserts.

The lower segment of a large permanent river arising outside the arid region through which it flows is a rapidly disappearing habitat because of impoundment. Thus, in the Colorado drainage there is no longer a Salt River or Gila River flowing through the Sonoran Desert, although headwater reaches persist in the mountains above various dams.

There is another modification of habitat not directly related to impoundment: salinity increase. In the lower Colorado River, changes have occurred that somewhat parallel those in the nearby Salton Sea. Salinity has increased in the river, not so much from evaporation and condensation as in the Salton, but rather from the pumping of subsurface saline water used for irrigation purposes. Similar changes have occurred to such an extent in the Rio Grande and Pecos River of Texas that marine fish are being stocked in reservoirs of that area (Minckley, 1965b). Thus, impoundment and contamination in arid America serve to blur the features of the normal fish zonation.

The upper reaches of some desert river systems are torrential streams in which there occur fish adapted for such an environment. Desquamation, cephalic dorsoventral flattening, terete and narrow caudal peduncles, falcate fins, and nuchal humping are typical of these fish. In western North America *Plagopterus argentissimus, Ptychocheilus lucius, Tiaroga cobitis,* and the humpbacked sucker *Xyrauchen texanus* are typical swift-water species. The most bizarre form, however, is *Gila cypha* (Miller, 1946) a Colorado River cyprinid that represents the extreme in the *Gila* complex showing ecological-morphological correlation (Fig. 12). *Gila robusta intermedia* from small tributaries is chubby bodied with comparatively large scales, small, rounded fins, and a deep caudal peduncle. In larger tributaries and small rivers the *G. r. robusta* form of this is intermediate between the first and the *G. r. elegans* form of swift river channels. *Gila cypha* from the Grand Canyon gorge is the culmination of the series with its inferior mouth, large fleshy snout, and conspicuous nuchal hump.

Hutchinson (1939) described comparable zonation in the river fish

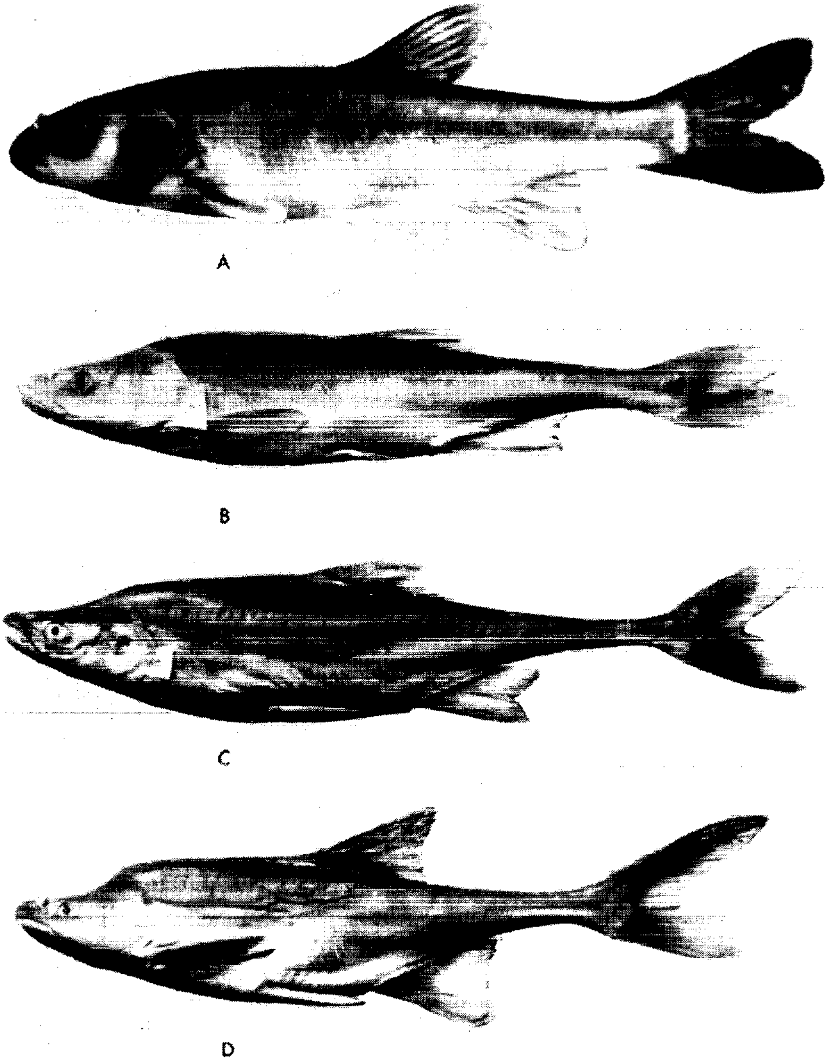

Fig. 12. Fish of the desert streams of Arizona. A: *Gila robusta intermedia*, typical of small streams with pools; B: *G. r. robusta*, typical of intermediate sized rivers; C: *G. r. elegans*, typical of large, swift rivers; D: *G. cypha*, typical of turbulent rivers. Courtesy of W. L. Minckley and R. R. Miller.

of Indian Tibet from the headwaters, where *Nemachilus* species and *Glyptosternum* occur, to the lacustrine swamps and slow rivers at lower altitudes. The most torrential reaches of the large streams are occupied by *Dyptichus maculatus* only. In other rapid, turbid rivers *Ptychobarbus conirostris* and *Oreinus sinuatus* occur.

The rivers of the endorheic Lahontan Basin originate as small, clear streams in the mountains, but they terminate as turbid and sluggish waters evaporating in saline–alkaline closed basins. The Truckee River, e.g., runs the gamut, dropping more than 800 meters from Lake Tahoe to Pyramid Lake. It shows analogous fish zonation. *Cottus beldingi* and *Prosopium williamsoni* occur in the headwaters; in the warmer, slower stretches *Catostomus tahoensis, Richardsonius egregius,* and *Siphateles bicolor* are found (La Rivers, 1962).

B. SIMILARITIES BETWEEN THE CASPIAN COMPLEX AND THE SALTON SEA

A comparison, albeit somewhat superficial, can be made between the old lakes of the Caspian Basin and the relatively new Salton Sea, California. Their saline waters contain ionic proportions different from seawater, although the Salton is comparable to the oceans in total salinity. They have been subject to natural and man-influenced invasions by marine and freshwater species, and pronounced instabilities in population structure seem to exist.

Arrival of the predatory Pacific muricid *Rapana bezoar* in the Black Sea had profound effects on the native pelecypods, and upon the distribution and habits of the fauna in general (Nikitin, 1962; Drapkin, 1964). The sand eel *Ammodytes cicerellus* now preys heavily on newly hatched *Rapana*, congregating in the snail spawning areas. In turn, the sea carp *Sargus annularius,* formerly a bottom feeder, now includes *Ammodytes* as an important item in its diet. Moreover, the hermit crab *Diogenes,* an exotic form from the Mediterranean, was unusually small in the Black Sea prior to the establishment of *Rapana.* Now *Diogenes* utilizes *Rapana* shells and attains normal dimensions, suggesting that the factor limiting its growth was available "house" size rather than low salinity as had been believed. The inadvertent transfer of *Mytilaster lineatus* from the Black Sea to the Caspian practically destroyed some molluscs in that body of water, with two species of *Dreissena* especially affected (Aligadzhiev, 1963). Also, the purposeful introduction of *Syndesmya ovata* from the Sea of Azov played a role in modifying the original Caspian fauna, although the total molluscan biomass may be about the same.

The faunal composition of the Salton Sea has changed markedly during its short life, and there is no reason to doubt that more changes will occur. Many changes have been associated with the increase in salinity since its maximum high surface level in 1907; others may be associated with annual temperature and chemical fluctuations, far greater than those of the marine environment, and the far-reaching effects of irrigation and impoundment (Carpelan, 1958). The original fish were from the Colorado River and by 1916 included the fresh-water *Gila robusta, Xyrauchen texanus, Salmo gairdneri,* and *Cyprinus carpio.* In addition, the euryhaline *Mugil cephalus* had gained entrance from the Gulf of California via the river and irrigation canals, and *Cyprinodon macularius* was present in a nearby spring. Within 15 years most freshwater species had disappeared, although *Cyprinodon* was common along the north shore and *Gambusia affinis* had appeared. Subsequent introductions failed except for that of the marine gobiid *Gillichthys mirabilis,* and by 1949 only four species were present. The construction of the Imperial Dam and the All-American Canal several years before had put an end to the recruitment of young mullets from the Gulf, and therefore *Mugil* was doomed.

Many Gulf species have been introduced since 1949, but only three survived and now seem to be established: *Cynoscion* is carnivorous and preys on *Bairdiella* and *Anisotremus.* By 1955 the threadfin *Dorosoma petenense,* an introduced forage fish, had moved from the Colorado River to the Salton and became another food item of *Cynoscion.* The basis for the seemingly firm establishment of this group of fish was the arrival of the polychaete *Neanthes succinea,* a benthic detritus feeder, upon which *Bairdiella* and *Anisotremus* depend. Superficially, this is somewhat like the situation in the Caspian Sea, where *Neanthes* was introduced as fish food, benefiting the sturgeon especially (Zenkevitch, 1963). The main difference is that complex food webs had existed in the Caspian prior to the arrival of *Neanthes.*

Currently, the Salton Sea and the Caspian Basin waters have a mixture of faunas. The Salton fish include the marine and freshwater forms discussed above, and recently *Mollienesia latipinnis* appeared. The barnacle *Balanus amphitrite, Neanthes,* and various planktonic diatoms, dinoflagellates, foraminiferans, and a tintinnid ciliate impart a marine aspect. Several blue–green algae, the rotifer *Brachionus plicatilis,* certain heleid flies, ephydrids, and corixids suggest inland waters. The rarest of the animals in the Salton Sea is probably *Cyclops dimorphus,* known only from that body of water (Johnson, 1953).

There has been adequate time for speciation to occur in the Caspian waters; e.g., 24 endemic polyphemid cladocerans have developed in the Pontocaspian Basin (Frey, 1965). These have arisen both from the freshwater *Bythotrephes* and the marine genus *Evadne.* In the young Salton Sea there is some suggestion that such changes are occurring also. The barnacle *Balanus,* first observed in 1942, has undergone considerable modification in shell structure and a new subspecies has been described from the Salton Sea (Rogers, 1949). Similarly, the foraminiferans are dwarfed and malformed, especially near freshwater inlets (Arnal, 1961). The status of *Cyclops dimorphus,* which must be considered an endemic on the basis of our present knowledge, invites speculation; it is closely allied to *C. bicolor,* and particularly *C. panamensis.* Environmentally induced modifications in morphology may be involved among the marine species in the Salton Sea, however, and caution must be applied in attributing these to genetic change.

VIII. Endemism, Relictism, and Special Habitats

Relictism and resultant endemism are common phenomena of deserts. Water-filled caves, springs, and marshes have served as refugia for aquatic animals in inhospitable areas that once were humid. A most spectacular case of relictism is the presence of crocodiles in pools in the Ahaggar Mountains of Africa, now surrounded by vast desert areas (see Beadle, 1943); in Australia at Lake Eyre, only fossil crocodiles are to be found today (Mawson, 1950).

Unique and endemic cirolanid isopods occur in rheocrenes of the Dead Sea rift (Pór, 1962b), in caves of the Edwards Plateau, Texas, in the Cuatro Ciénegas bolson (Cole and Minckley, 1966), and elsewhere in Mexico (Bowman, 1964). The unusual crustacean order Thermosbaenacea is also represented by endemic species in the Jordan Depression (Pór, 1962a), hot springs in south Tunis (a region of North Africa that has a history similar to that of the Dead Sea rift), and in the Texas caves (Maguire, 1965).

A bizarre situation occurs northwest of the bleak Kalahari desert where the stunted, endemic clariid catfish, *Clarias cavernicola,* lives in a dark sink. It feeds on the excreta of baboons living in a dry cave above the sink (Jubb, 1965). Occurrence of ictalurid catfish in subterranean waters of desert and semidesert areas is also known in the American Southwest (Hubbs and Bailey, 1947; Carranza, 1954).

Four species of the harpacticoid copepod genus *Nitocra* have survived in waters of Israel's Jordan Valley (Pór, 1964). *N. balnearia* occurs only in the hot springs of Hamei Zohar (5.6% salinity). It was probably derived from a species that entered the valley during a marine transgression and lived in the Dead Sea until increasing salinity precluded survival there. *N. hibernica* and *N. incerta* coexist in Lake Tiberias, clearly partitioning the littoral environment; *N. lacustris* is a member of the Tiberias psammon.

The Ein Feshka area in Palestine is a marshy stretch of about 1 km^2 on the northwest coast of the Dead Sea. The area has been long isolated from other freshwaters and members of the local population of fish, the cichlid *Tilapia nilotica* and two cyprinodonts, *Aphanius dispar* and *A. sophiae,* show distinct features (Steinitz, 1951a). At least the cichlid has been described as a new subspecies (Steinitz, 1951b).

Closed, isolated basins of the Anatolian Plateau harbor cyprinodont fish referable to *Aphanius* and the similar *Anatolichthys* that were in contact with one another during most of the Tertiary and Pleistocene (Kosswig, 1961). Some lakes are so saline that no fish occur there, but they are restricted to influent streams or nearby springs along with a unique molluscan fauna. Differences have arisen among the separate populations, but in unusually wet years saline pools link the different springs, permitting genetic exchange among them. In Lake Burdur, rich in $MgSO_4$, there is a hybrid swarm showing features of both genera; apparently, other genotypes cannot survive there. *Arctodiaptomus burduricus* is abundant and endemic to the lake.

Similarly, in the Cuatro Ciénegas basin of Coahuila, populations of cichlids, cyprinodonts, and other fish (18 species, at least 10 of which are endemic) persist in various springs that arise from the desert floor, formerly the bottom of a large pluvial lake or of lakes. Irrigation and water diversion have served to bring together various populations with subsequent hybridization (Minckley, 1965a). The entire bolson of Cuatro Ciénegas is remarkable for its endemic fauna of which the gastropods are most noteworthy (Taylor, 1966). Thirteen species of hydrobiid snails occur; 12 are new endemics, included in five new genera and three new subfamilies. No more spectacular endemic fauna of freshwater gastropods is known in the western hemisphere. Also, a box tortoise, *Terrapene coahuila,* has survived as a relict in the basin by becoming aquatic (Webb *et al.,* 1963) and has evolved a carapace remarkably like that of *Kinosternon,* presumably in response to its habitat in close-spaced marsh vegetation.

The native freshwater fish of western North America include a complex of endemic faunas sharing relatively few widespread species; in addition, many relict, monotypic genera are present (Miller, 1961b). In Death Valley, once filled by pluvial Lake Manly, there are three fish families, including five genera and 10 species; nine species are endemics and six of these are cyprinodonts. *Cyprinodon diabolis,* e.g., is represented by a population of 100–400 individuals confined to a single spring hole in water of 34°C. The rate of speciation in such small, isolated populations may be enhanced by genetic drift, and in hot springs there may be continuous reproduction producing several generations a year.

Warm water generally brings about changes in meristic characters. Scales and fin rays, especially, are reduced in numbers (Miller, 1948). *Tellia apoda,* a cyprinodont of North Africa, lacks pelvic fins and occurs in slightly saline, warm springs (Beadle, 1943). Hubbs (1959) reported increased frequency of anomalies in *Gambusia affinis* from warm pools.

The fish of hot-springs are extraordinarily tolerant to low oxygen; *Crenichthys baileyi* and *C. nevadae* are especially hardy, showing no distress in water over 30°C with less than 1 mg/liter dissolved oxygen (Hubbs and Hettler, 1964). Thermal barriers limit the distribution of these warm-water forms; *C. baileyi* and the Moapa dace, *M. coriacea,* another species which tolerates low oxygen tensions, are clearly restricted by low-temperature barriers (La Rivers, 1962). *Cyprinodon macularius,* the desert pup fish, inhabits water up to 48.9°C (Miller, 1948), but is not especially stenothermal.

The converse of relictism and endemism is the occurrence of unique but widely distributed species in arid zones. In desert areas, man's canalization and impoundment of water has led to the creation of relatively new and artificial habitats—perhaps many more than in humid regions (Pennak, 1958). It is not surprising that certain, almost cosmopolitan animals typical of such habitats occur in desert waters. The hydrozoan *Craspedacusta sowerbyi* in Lake Mead (Deacon and Haskell, 1963) and the tubificid *Branchiura sowerbyi* from Saguaro Lake and an irrigation canal in Arizona (Cole, 1966a) are two such animals.

The lack of species diversity in isolated desert habitats, and particularly in springs, has resulted in the evolution of forms that are extremely susceptible to exotic introductions. Hubbs and Brodrick (1963) have shown that an introduced competitor species is a more serious hazard to the original population than is an invading predator. Additional documentation for the reduction of native, desert fish in response to purposeful exotic introduction can be found in the works of Hubbs and Hettler (1959), Miller (1961a, 1965), Miller and Lowe (1964), Deacon *et al.* (1964), and Hubbs and Deacon (1964). There are several other reasons for the changing pattern of fish fauna in arid North America for which man must accept blame (Miller, 1961a). At present—with the activities of uninformed laymen, with state and federal sports–fishery departments constantly introducing exotics, often after applying rotenone to remove "rough fish," and with Public Health personnel distributing *Gambusia affinis* widely for mosquito control—the future is especially bleak, not only for fish, but perhaps also for the little-studied invertebrates of the North American desert.

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