

Part 6. Wetlands

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Desert Plants

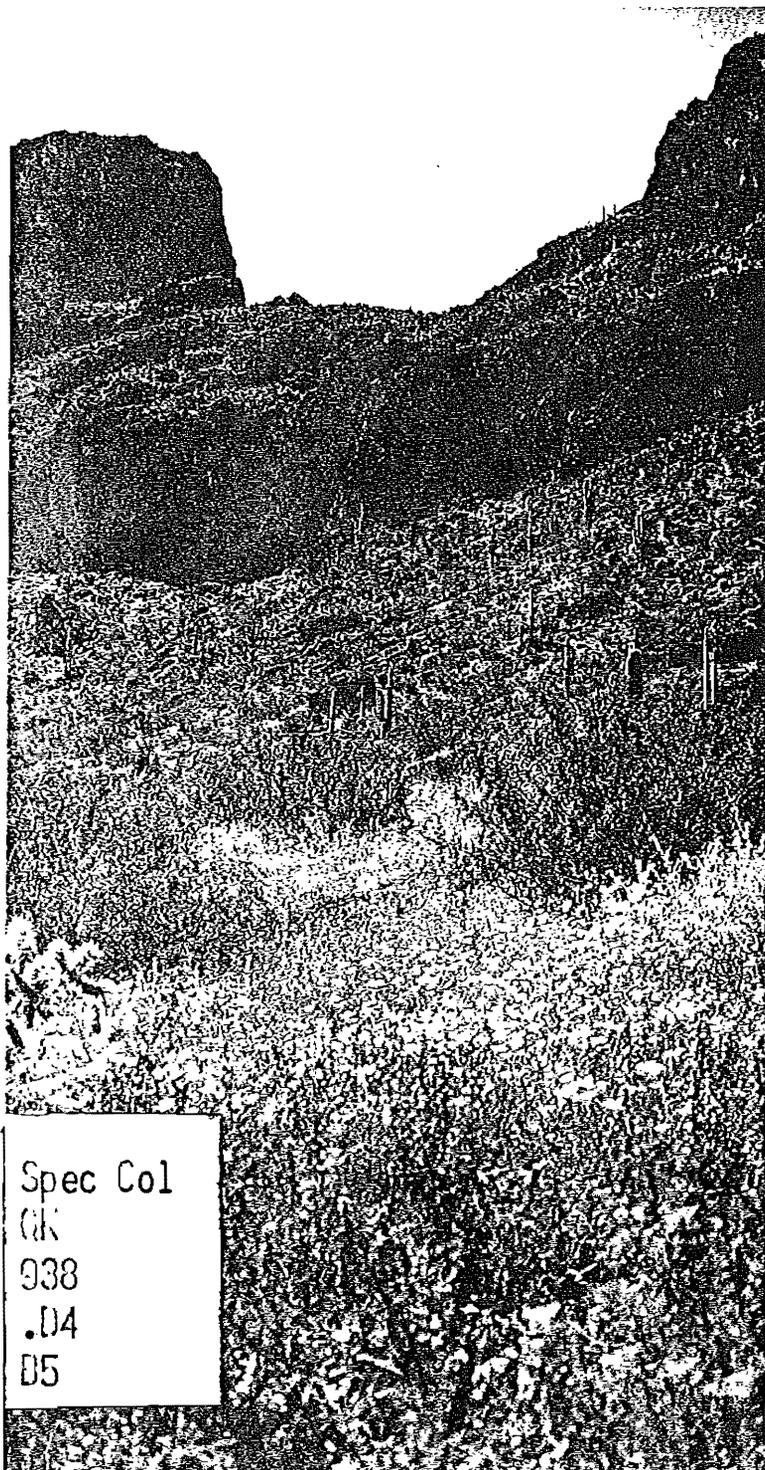
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Special Issue

Biotic Communities of the American Southwest—United States and Mexico

David E. Brown
Editor



Picacho Peak State Park. Photo by Josh Young.

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Figure 143. Integration of aquatic and riparian communities - only emergent aquatic plants (marshlands) are absent, and they occurred a few hundred meters from this site. Submergent (mostly the alga *Cladophora glomerata*) and strand (barren) habitats, lined by riparian scrub (*Baccharis salicifolia*), subtropical deciduous woodland (*Prosopis velutina*), and warm temperate riparian broadleaved forest [*Populus fremontii*, *Salix* spp., etc]. Bonita Creek, Graham County, Arizona. Elevation ca. 960 m; photograph by Stuart G. Fisher, June 1979.

Southwestern Wetlands

Wetlands are periodically, seasonally, or continuously submerged landscapes populated by species and/or life forms differing from immediately adjacent biotas. They are maintained by and depend upon circumstances more mesic than those provided by local precipitation. Such conditions occur in or adjacent to drainage-ways and their floodplains (riparian zones), on poorly drained lands, along seacoasts, and in and near other hydric and aquatic situations, i.e., springs and their outflows, ponds, margins of lakes, etc. The various wetland and riparian communities may be represented as forest, woodland or scrubland, marshland or strand, or be composed largely or entirely of submergent vegetation (Fig. 143).

Although wetland formations may be remarkably distinct, they are also often highly integrated, or occur as intermittent stands within other communities (Fig. 144). In riparian habitats that pass through many biomes, high elevation species often extend downslope into grassland or desert within canyons that lead cooler and moister air downward (Lowe 1964; Fig. 145). Also, formations encountered are often

successional as a result of periodic disturbance from flood scouring, inundation, desiccation, grazing by animals, or other factors. The communities and associations are dynamic, subject to frequent change, displacement, replacement, and succession (Campbell and Green, 1968; Everitt, 1968; Johnson et al, 1976; Reichenbacher, 1980).

Although formation-classes of wetland habitats may frequently be complex, the number of dominants often is surprisingly few, especially of aquatic plants where monospecific stands (consociations) are remarkably recurrent in time and space (Gessner, 1955 et seq.). Growth of aquatic and semiaquatic plants is rapid, and succession to at least a quasi-climax may occur in a period of weeks or months.

Aquatic, riparian and other wetland biotic communities of the American Southwest have rarely been differentiated or shown on maps. They tend to be small relative to other communities, but possess an importance and biological interest totally disproportionate to their limited geographic occurrence.

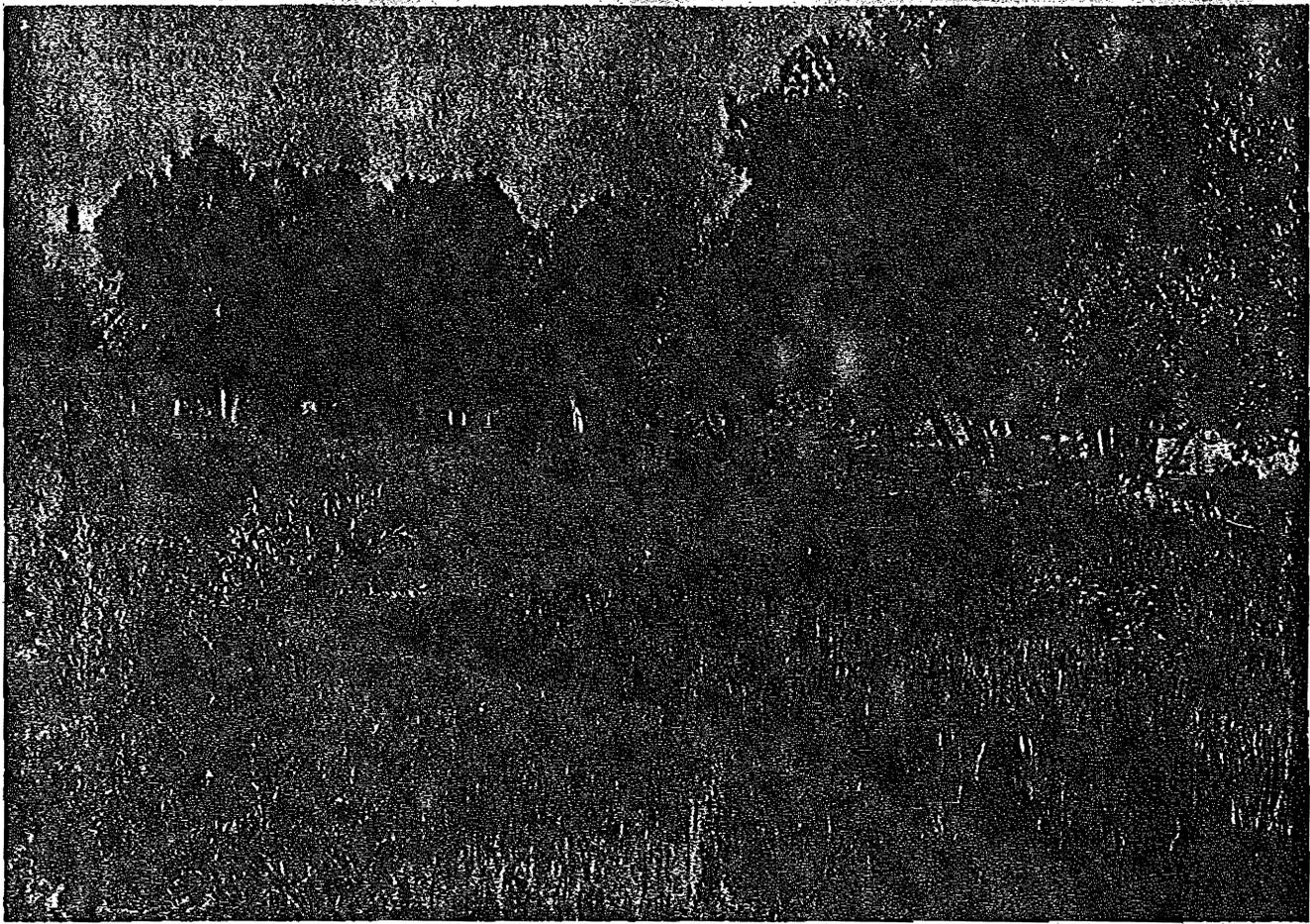


Figure 144. Integration of aquatic and riparian communities— cold temperate marshland (*Scirpus* spp.), cold temperate woodland (Red Willow, *Salix laevigata*), submergent (open water) and at left, mostly out of the picture, scrubland communities. Meadow Valley Wash north of Prescott, Yavapai County, Arizona. Elevation ca. 1,800 m.

Physical Environments of Southwestern Wetlands

The Southwest's major rivers (Fig. 146) have been altered by dams for many years, their flows diverted and changed, and their once-perennial lower reaches de-watered (Deacon and Minckley, 1974). In fact, the Southwest's largest river, the Colorado, with the exception of a few important reaches (Figs. 147, 148), has been reduced to a series of impoundments connected by canals. These regulated streams have much of their former nutrient loads trapped by reservoirs, to the detriment of downflow systems (Paulson and Baker, 1980). Further, discharge, temperature, and sedimentation regimes are now unsuitable for a native aquatic and semi-aquatic biota adapted to a seasonably turbid and variably aggrading and degrading, warm, and vernal-flooded system (Minckley, 1979). Their highly specialized, endemic fish faunas have been largely destroyed and replaced by non-native species [see e.g. Miller, 1961; Minckley and Deacon, 1968; Moyle and Nichols, 1973]. Some lesser rivers are as yet unregulated, however, and these along with many smaller streams at intermediate elevations still support native aquatic faunas variously influenced by introduced forms.

Prior to 1880, alluvial plains of river bottoms at lower elevations (<1,000 m) were wetter and less well drained than at present. Streams were commonly characterized by boggy margins, marshy sloughs, and backwaters (Fig. 149), which

were of great annoyance to early travelers and a health hazard to personnel at 19th Century military posts (Hastings, 1959). Stream channels were typically shallow and braided, with deeper water in meanders and oxbows, and where Beaver (*Castor canadensis*) activity was prevalent (Davis, 1982). The well known but poorly understood cycle of arroyo cutting (Fig. 150) that began in the 1880's and 1890's (Bryan, 1925a, 1928; Cooke and Reeves, 1976; Leopold, 1976), coupled with deliberate river channelization, streamflow impoundment and diversion, and mining of ground water, have caused these riverine and adjacent spring-fed marshlands (*ciénegas*) to become an almost extinct Southwestern landscape feature.

Natural lakes and ponds, other than those associated with local fluvial action, are rare in the Southwest. This results largely from a lack of recent glaciation, general aridity, high evaporation and siltation rates, and the steep gradients of much of the topography. With the exception of some high-elevation glacial lakes in southwestern Colorado, most smaller natural lakes (*lagunas*) are sinkholes resulting from solution and gradual erosion of soluble, underlying rocks (Cole, 1963, 1968). Subsidence basins resulting from underflow or degassing of lava are locally present, and the resulting calderas may hold transitory or permanent waters. Larger lakes are (or were in the past) mostly tectonic in origin, occupying closed basins (*bolsones*) or occurring as a result of structural uplift that impounded ancient waterways. Most are presently more or less marshy and seasonal.

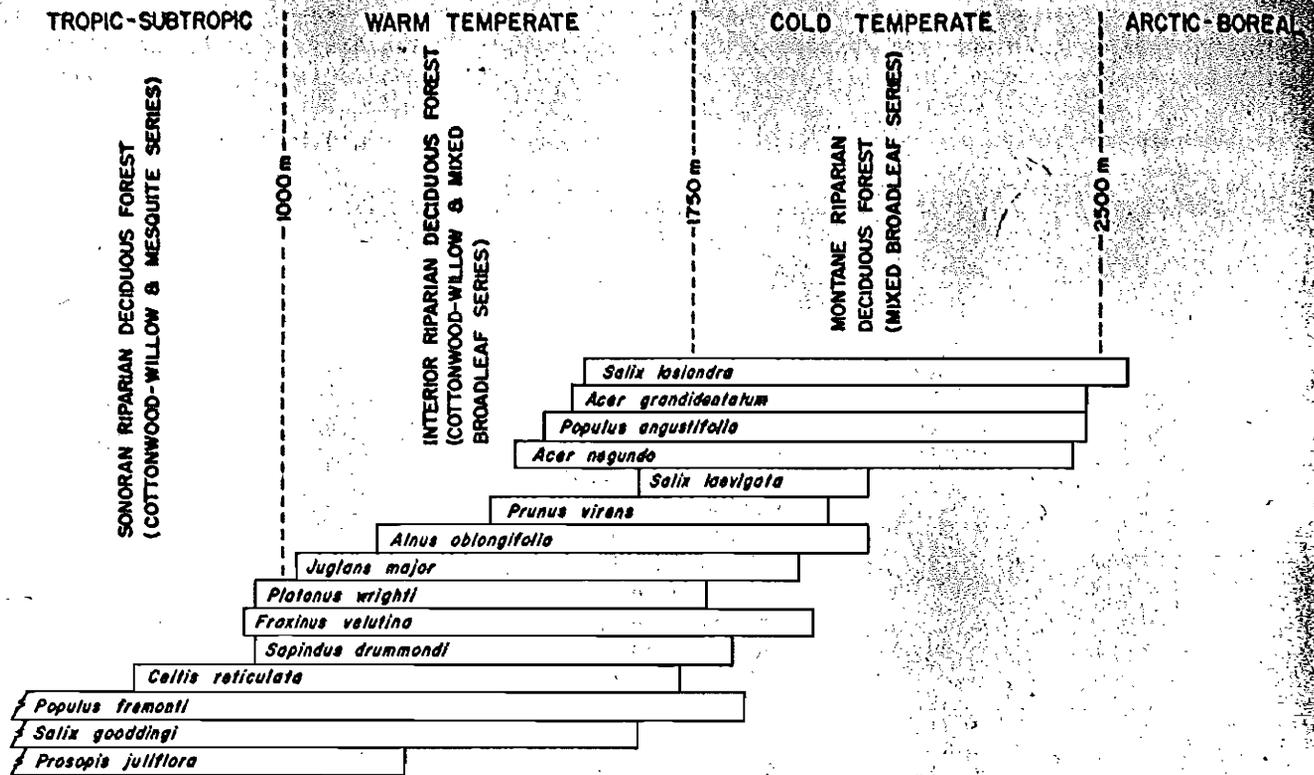


Figure 145. Generalized altitudinal, climatic and community distribution for some deciduous riparian trees in the sub-Mogollon Rim region of central Arizona.

Most large, natural lentic habitats in the Southwest are endorheic, fed by ephemeral inflows and by definition lacking surface outflows. Water passes out of such systems by evaporation and/or downward percolation if the lake is perched above the groundwater table. Such lakes often are saline, and although they are heavily populated by diverse invertebrates and, therefore, attractive to waterfowl, shorebirds and wading birds, provide little habitat for fishes. Normally dry, closed basin lakes are called *playas*. Although commonly considered characteristic landscapes of the Chihuahuan Biotic Province, *playas* are found in all four North American deserts, and throughout the Southwest. Two of the largest of these—the Salton Sea in California and Laguna Salada in Baja California del Norte—have been, or are in the process of being, transformed into permanent bodies of water through diversion of Colorado River water.¹ Some smaller closed basin lakes at higher elevations, with attendant increased precipitation and reduced evaporation, provide relatively dependable aquatic habitats (e.g., Mormon Lake in Arizona, elevation ca. 2,150 m; Lake Elsinore in California, ca. 1,000 m). A few depressions, such as Laguna Prieta in northwestern Sonora, that intersect groundwater tables thus remain relatively permanent (Fig. 151).²

Rockpools (*tinajas*) in arid mountain ranges have long been known as oases critical for survival of ancient peoples (Taylor,

1962) and for later desert travelers (Bryan, 1925b). They also support local and often distinctive populations of plants, invertebrates, and vertebrates [the last ranging from amphibians through large mammals such as Bighorn Sheep]. These small habitats, typically scoured from bedrock by boulders powered by infrequent flash floods, qualify as special wetlands within the Southwest's myriad of systems (Fig. 152). They are so poorly known biologically that we scarcely treat them further, but seepages downslope from such places may support diverse and special riparian communities—dense stands of cottonwood and willow may be present at some locales, or groves of palms in places like the Kofa Mountains of Arizona.

Far more numerous than natural freshwater habitats are artificial reservoirs (*presas*), farm ponds (*estanques*) and the innumerable cattle tanks (*repesos* or *charcos*) of varying degrees of permanence. These, and pumped ponds, have created a scattering of aquatic communities in arid parts of the Southwest that were otherwise devoid of surface water. Such impoundments created lentic habitats in a region formerly dominated by streams.

Extensive canal systems provide linear, flowing systems across desertlands, often interconnecting formerly isolated bodies of water to allow dispersal of organisms across vast reaches formerly denied to them, and also providing a transportation system for terrestrial organisms and their propagules. Lining of canals with concrete in the past few years has drastically reduced these substitute riparian habitats by suppressing seepage, and their steep-walled channels often become a death trap for desert animals.

Springs, some within *bolsones*, have provided aquatic habitats for a large percentage of the unique "desert" fishes of

¹For an informative account of the filling of the Salton Sea see Sykes (1937), *The Colorado Delta*.

²Recent photographs (1979) of Laguna Prieta show it to be almost dry, probably as a result of normal annual fluctuation but possibly also the result of new water-well fields in the vicinity.



Figure 147. Aerial view of the Colorado River mainstream between Parker, Yuma County, Arizona, and Blythe, Riverside County, California, a reach yet to be severely modified by channelization, levees, and dredging. Floodplain vegetation where undisturbed by agriculture consists of subtropical deciduous woodland (*Prosopis velutina*, *P. pubescens*, *Tamarix chinensis*, etc.) and a complex scrubland of diverse genera (*Atriplex*, *Baccharis*, *Pluchea*, *Tessaria*, *Tamarix*, etc.). Riparian deciduous forests of Cottonwood (*Populus fremontii*) and Willow (*Salix gooddingii*) persist as small stands not visible in the photograph, and marshlands (*Scirpus californicus*, *S. americanus*, *Typha domingensis*, and many others) line the submergent communities of the river. Elevation ca. 210 m; photograph by Robert D. Ohmart, 1976.

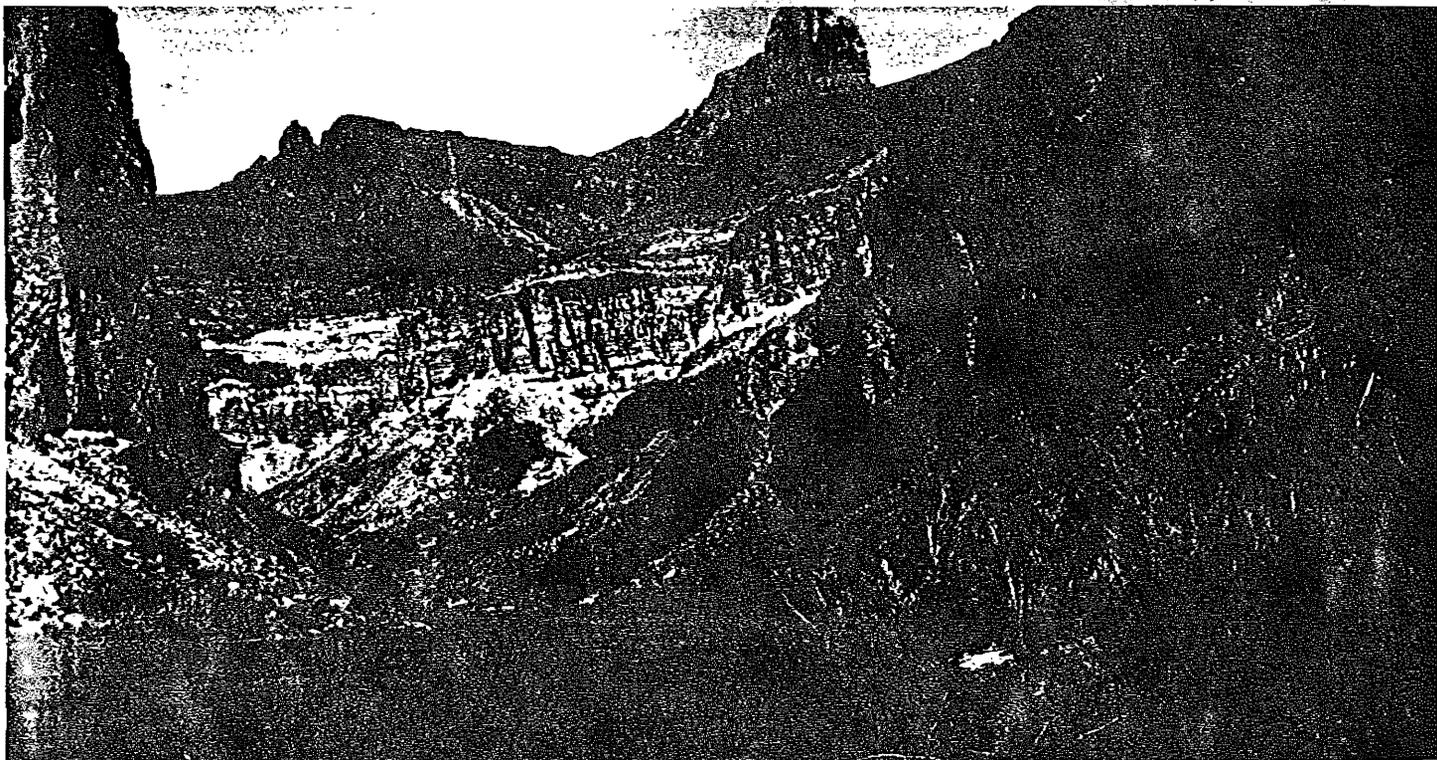


Figure 148. Colorado River mainstream in Grand Canyon National Park, Coconino County, Arizona. Although the river now is controlled by Glen Canyon Dam, closed in the early 1960's, a border of riparian scrub (principally *Prosopis velutina*) above the zone of scour by flooding in years past remains evident. Elevation ca. 500 m; photograph by W.L. Minckley, August 1978.



Figure 149. Interior view of mature ciénega habitat at Atascosa, Sonora, México. Submergent communities were principally of algae, with emergent *Polygonum* spp., *Salix gooddingii* and marginal *S. exigua* and sedges [*Scirpus* spp.]. Elevation ca. 1,200 m; photograph by Gary Meffe, July 1980.

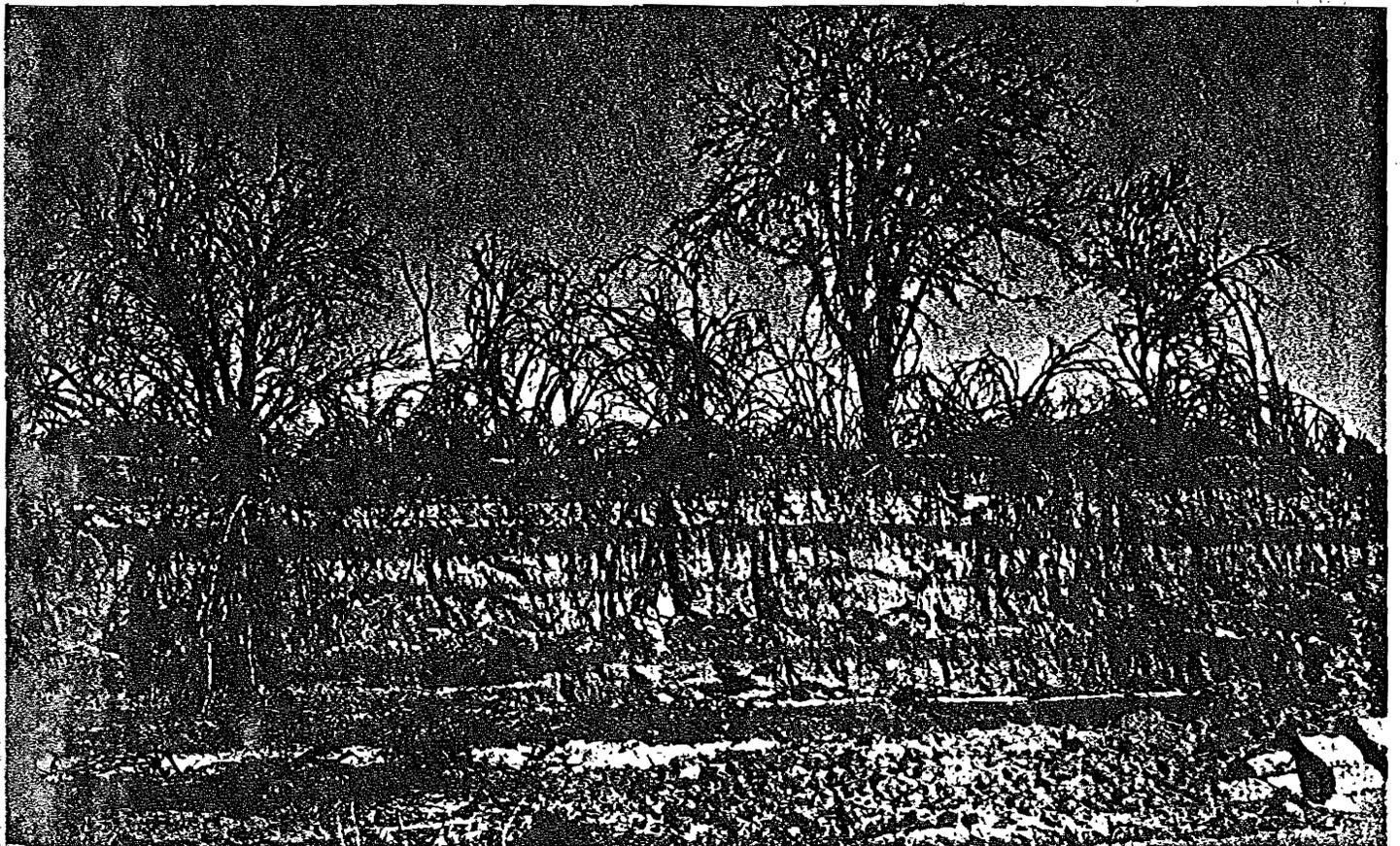


Figure 150. Cut banks and dead mesquites along Santa Cruz River, near San Xavier, Pima County, Arizona. Once one of the finest mesquite bosques in the Southwest, ground water pumping has now virtually destroyed this interesting community.

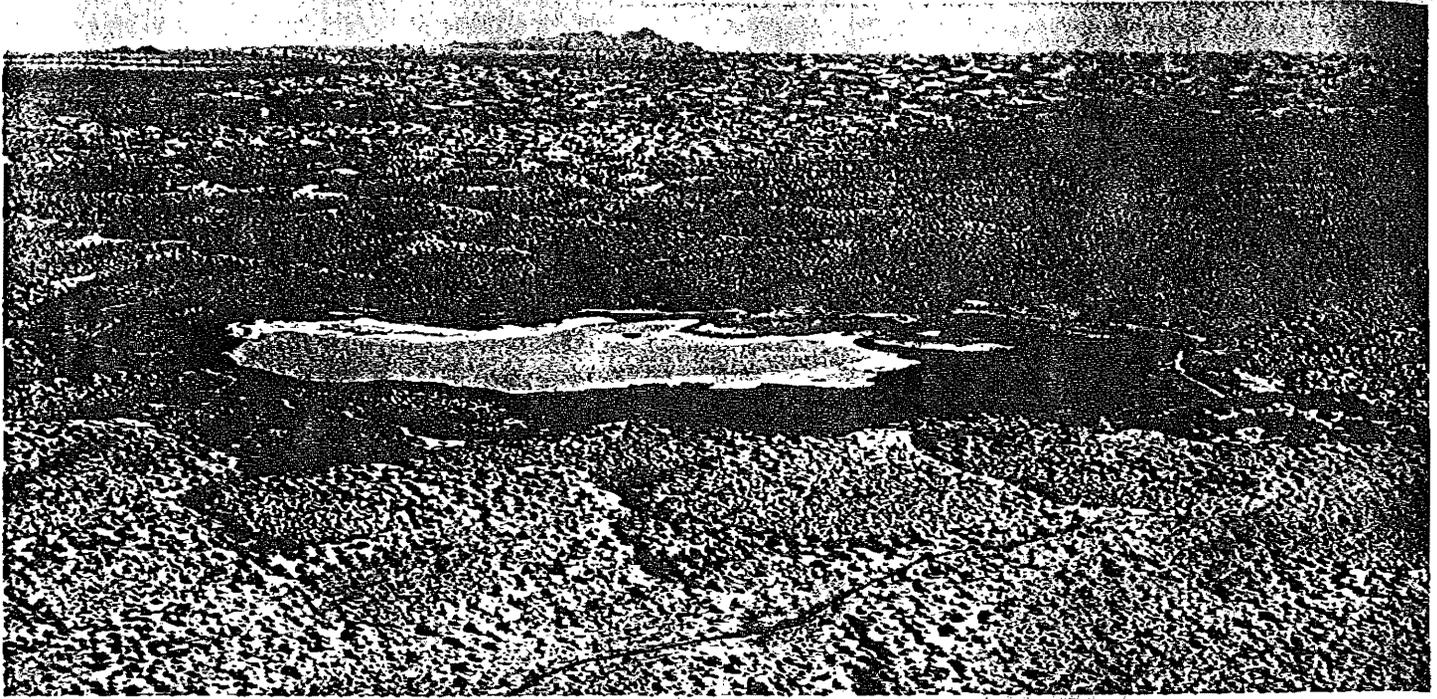


Figure 151. *Laguna Prieta, a permanent lake in the Gran Desierto region of the Sonoran Desert, Sonora Mexico. Sierra Del Rosario is in left center background. A surprise is the presence here of a natural lake, albeit saline, fed by springs, and of a high water table in such an arid region. Elevation ca. 50 m; photograph by Peter Kresan.*

Problems with Classification of Aquatic Habitats

Because lakes and large bodies of quiet water were unusual and typically ephemeral in the recent Southwest, the region's unique aquatic biota became largely stream adapted, or was physically restricted to remnant springs and seeps. Thus, although the evolution of aquatic organisms has not been completely independent of terrestrial changes in the Southwest, relationships of such differentiation to terrestrial biomes are often obscure. Numbers of fish species present in a particular drainage basin, for example, depends more on geologic, climatic, and evolutionary histories, and size and complexity of the watershed, than on elevation or terrestrial vegetation.

The ecology of aquatic systems, while differing substantially from terrestrial habitats, is not entirely independent of climate. Streams originating in Arctic-Alpine areas flow downslope through other biomes, and some aquatic species occupy a number of defined (or definable) zones of terrestrial landscape. Physiological constraints obviously restrict such animals as trouts to cool waters at higher altitudes. Other fish groups of tropical or marine affinities (e.g., cyprinodontids and poeciliids) are similarly restricted to lower, warmer places. A vast majority of native fishes present in the Southwest, however, consists of the minnow and sucker families (Miller, 1959), an array of diversity that precludes the luxury of generalizations. Exceptions to these rules also occur when special habitats such as thermal springs are at high elevations, or deep, cool lakes are present in deserts. Also, special conditions such as downcanyon drainage of cool, montane air may allow cold-water fishes, other animals, and riparian plants to penetrate far into other biomes. Some species are thus included in discussions of characteristic biotic elements of more than one biome—far more in this section than is the case elsewhere in the text.

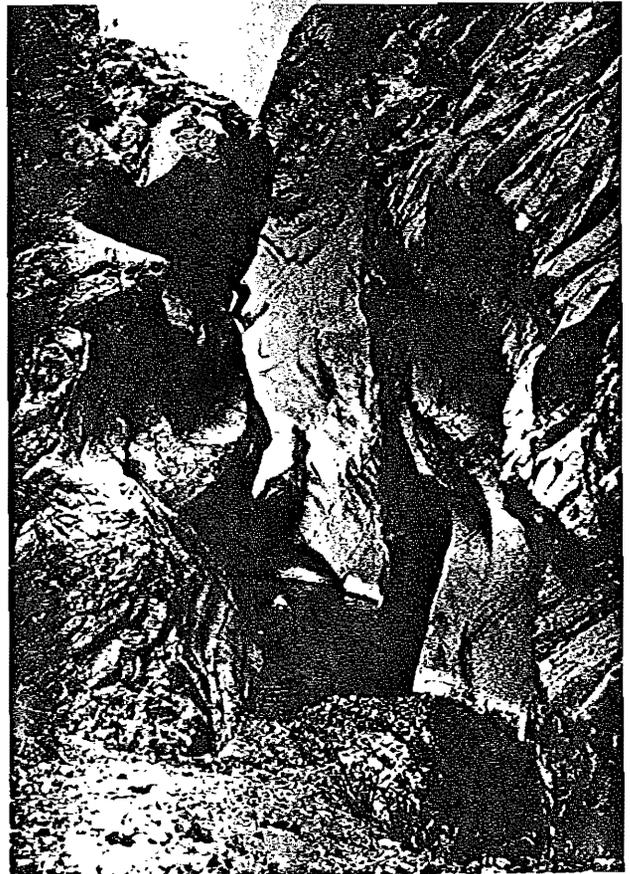


Figure 152. *Permanent rockpool [tinaja] in the Hieroglyphic Mountains, Maricopa County, Arizona, a habitat too erosive to support other than algae and other transitory plants, but extremely important as a water supply to numerous desert animals. Elevation ca. 680 m.*

Table 32. Distribution of native, freshwater fishes in drainage basins of the American Southwest.

Species	Plains ^a	Rio Grande basin			Rio Conchos	Guzman Basin ^b	Rio Yaqui	Coastal drainages		Death Valley System	Colorado River basin		
		Pecos River ^c	Upper ^d	Lower ^d				Baja California ^e	Pacific Coast ^f		Lower ^g	Gila River	Middle ^h
Petromyzontidae (Lampreys)													
<i>Lampetra tridentata</i> (Pacific Lamprey)	-	-	-	-	-	-	-	-	X	-	-	-	-
Acipenseridae (Sturgeons)													
<i>Scaphirhynchus platyrhynchus</i> (Shovel-nosed Sturgeon)	X ^a	-	X	X	-	-	-	-	-	-	-	-	-
Lepisosteidae (gars)													
<i>Lepisosteus oculatus</i> (Spotted Gar)	X ^a	X	X	X	-	-	-	-	-	-	-	-	-
<i>L. osseus</i> (Longnose Gar)	X ^a	X	X	X	X	-	-	-	-	-	-	-	-
Clupeidae (shads)													
<i>Dorosoma cepedianum</i> (Gizzard Shad)	X	X	X	X	X	-	-	-	-	-	-	-	-
<i>D. smithi</i> (Pacific Shad)	-	-	-	-	-	-	X	-	-	-	-	-	-
Elopidae (Tenpounders, Tarpons)													
<i>Elops affinis</i> (Machete)	-	-	-	-	-	-	X	-	-	-	X	X	-
Salmonidae (Salmon, Trouts, Whitefishes)													
<i>Prosopium williamsoni</i> (Mountain Whitefish)	-	-	-	-	-	-	-	-	-	-	-	-	X ^c
<i>Salmo apache</i> (Arizona Trout)	-	-	-	-	-	-	-	-	-	-	-	X	X
<i>S. gairdneri</i> (Rainbow Trout)	-	-	-	-	-	-	-	X	X	-	-	-	-
<i>S. gilae</i> (Gila Trout)	-	-	-	-	-	-	-	-	-	-	-	X	-
<i>Salmo</i> sp. (Yaqui Trout)	-	-	-	-	-	X	X	-	-	-	-	-	-
Characidae (Tetras)													
<i>Astyanax mexicanus</i> (Mexican Tetra)	-	X	X	X	X	-	-	-	-	-	-	-	-
Cyprinidae (Carp, Minnows)													
<i>Agosia chrysoaster</i> (Longfin Dace)	-	-	-	-	-	-	X	X	-	-	-	X	-
<i>Compostoma anomalum</i> (Plains Stoneroller)	X	-	-	X	-	-	-	-	-	-	-	-	-
<i>C. ornatum</i> (Mexican Stoneroller)	-	-	-	X	X	X	X	X	-	-	-	-	-
<i>Codoma ornata</i> (Ornate Minnow)	-	-	-	-	X	-	X	-	-	-	-	-	-
<i>Dionda diaboli</i> (Devil's River Minnow)	-	-	-	X ^b	-	-	-	-	-	-	-	-	-
<i>D. episcopa</i> (Roundnosed Minnow)	-	X	X	X	X	-	-	-	-	-	-	-	-
<i>Gila bicolor snyderi</i> (Owens Tui Chub)	-	-	-	-	-	-	-	-	-	X	-	-	-
<i>G. bicolor mohavensis</i> (Mohave Chub) ¹¹	-	-	-	-	-	-	-	-	-	X	-	-	-
<i>G. cypha</i> (Humpback Chub)	-	-	-	-	-	-	-	-	-	-	X	-	X
<i>G. ditaenia</i> (Sonora Chub)	-	-	-	-	-	-	-	X	-	-	-	-	-
<i>G. elegans</i> (Bonytail Chub)	-	-	-	-	-	-	-	-	-	-	X	X	X
<i>G. intermedia</i> (Gila Chub)	-	-	-	-	-	-	-	-	-	-	-	X	-
<i>G. nigrescens</i> (Guzman Chub)	-	-	-	-	-	X	-	-	-	-	-	-	-
<i>G. orcutti</i> (Arroyo Chub)	-	-	-	-	-	-	-	-	X	-	-	-	-

Species	Plains ¹	Rio Grande basin				Guzman Basin ²	Rio Yaqui	Coastal drainages		Death Valley System	Colorado River basin			
		Pecos River ¹	Upper ¹	Lower ¹	Rio Conchos			Baja California ⁴	Pacific Coast ⁵		Lower ³	Gila River	Middle ⁶	Upper ¹¹
<i>G. pandora</i> (Rio Grande Chub)	-	X	X	-	-	-	-	-	-	-	-	-	-	-
<i>G. pulchra</i> (Mesa del Norte Chub)	-	-	-	-	X	-	X	-	-	-	-	-	-	-
<i>G. purpurea</i> (Yaqui Chub)	-	-	-	-	-	-	X	X	-	-	-	-	-	-
<i>G. robusta</i> (Roundtail Chub)	-	-	-	-	-	-	X	-	-	-	X	X	X	X
<i>Hybognathus nuchalis</i> (Silvery Minnow)	X	X	X	X	X	-	-	-	-	-	-	-	-	-
<i>H. plucitus</i> (Plains Minnow)	X	X	X	X	-	-	-	-	-	-	-	-	-	-
<i>Hybopsis aestivalis</i> (Speckled Chub)	X	X	X	X	X	-	-	-	-	-	-	-	-	-
<i>Lepidomeda albivalis</i> (White River Spinedace)	-	-	-	-	-	-	-	-	-	-	-	-	X	-
<i>L. altivelis</i> (Pahrnagat Spinedace)	-	-	-	-	-	-	-	-	-	-	-	-	X	-
<i>L. mollispinis</i> (Middle Colorado Spinedace)	-	-	-	-	-	-	-	-	-	-	-	-	X	-
<i>L. vittata</i> (Little Colorado Spinedace)	-	-	-	-	-	-	-	-	-	-	-	-	X	-
<i>Meda fulgida</i> (Spikedace)	-	-	-	-	-	-	-	-	-	-	-	X	-	-
<i>Notropis amabilis</i> (Texas Shiner)	-	X	X	X	X	-	-	-	-	-	-	-	-	-
<i>N. braytoni</i> (Tamaulipan Shiner)	-	X	X	X	X	-	-	-	-	-	-	-	-	-
<i>N. buchanani</i> (Ghost Shiner)	X ^a	-	-	X	-	-	-	-	-	-	-	-	-	-
<i>N. chihuahuana</i> (Chihuahuana Shiner)	-	-	-	X	X	-	-	-	-	-	-	-	-	-
<i>N. formosus</i> (Beautiful Shiner)	-	-	-	-	-	X	X	-	-	-	-	-	-	-
<i>N. girardi</i> (Arkansas River Shiner)	X ^a	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>N. jemezianus</i> (Rio Grande Shiner)	-	X	X	X	X	-	-	-	-	-	-	-	-	-
<i>N. lutrensis</i> (Red Shiner)	X	X	X	X	X	-	-	-	-	-	-	-	-	-
<i>N. panatcys</i> (Conchos Shiner)	-	-	-	-	X	-	-	-	-	-	-	-	-	-
<i>N. proserpinus</i> (Prosperine Shiner)	-	X	X	X ^b	-	-	-	-	-	-	-	-	-	-
<i>N. rutilus</i> (Salado-San Juan Shiner)	-	-	-	X ^b	-	-	-	-	-	-	-	-	-	-
<i>N. shumardi</i> (Silver-band Shiner)	X ^a	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>N. simus</i> (Bluntnose Shiner)	-	-	X	X	-	-	-	-	-	-	-	-	-	-
<i>N. stramineus</i> (Sand Shiner)	X	X	-	X	-	-	-	-	-	-	-	-	-	-
<i>N. venustus</i> (Spot-tail Shiner)	-	-	-	X ^b	-	-	-	-	-	-	-	-	-	-
<i>Phenacobius mirabilis</i> (Suckermouth Minnow)	X	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Phoxinus erythrogaster</i> (Red-bellied Dace)	X ^a	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pimephales promelas</i> (Flathead Minnow)	X	X	X	X	X	X	-	-	-	-	-	-	-	-
<i>Plagopterus argenteus</i> (Woundfin)	-	-	-	-	-	-	-	-	-	-	X	X	X	-

Species	Plains ¹	Rio Grande basin			Guzman Basin ³	Rio Yaqui	Coastal drainages		Death Valley System	Colorado River basin		
		Pecos River ²	Upper ¹	Lower ⁴			Rio Conchos	Baja California ⁴		Pacific Coast ⁵	Lower ⁶	Gila River
<i>G. xatzei</i> (Big Bend Gambusia)	-	-	-	X	-	-	-	-	-	-	-	-
<i>G. hurtadoi</i>	-	-	-	-	X	-	-	-	-	-	-	-
<i>G. krumholzi</i> (Krumholz Gambusia)	-	-	-	X ^b	-	-	-	-	-	-	-	-
<i>G. nobilis</i> (Pecos Gambusia)	-	X	-	X	-	-	-	-	-	-	-	-
<i>G. senilis</i> (Blotched Gambusia)	-	-	-	X	X	-	-	-	-	-	-	-
<i>Poeciliopsis monacha-occidentalis</i>	-	-	-	-	-	X	X	-	-	-	-	-
<i>P. occidentalis</i> (Sonora Topminnow)	-	-	-	-	-	X	X	-	-	-	X	-
<i>P. prolifica</i>	-	-	-	-	-	X	-	-	-	-	-	-
Atherinidae (Siversides)												
<i>Menidia audens</i> (Mississippi Silverside)	X ⁴	-	-	-	-	-	-	-	-	-	-	-
<i>M. beryllina</i> (Tide-water Silverside)	-	-	-	X ^b	-	-	-	-	-	-	-	-
Gasterosteidae (Sticklebacks)												
<i>Gasterosteus aculeatus</i> (Threespine Stickleback)	-	-	-	-	-	-	X	-	-	-	-	-
Percichthyidae (Temperate Basses)												
<i>Morone chrysops</i> (White Bass)	X ⁴	X	-	X	-	-	-	-	-	-	-	-
Centrarchidae (Sunfishes)												
<i>Chaenobryttus gulosus</i> (Warmouth)	X ⁴	X	-	X	-	-	-	-	-	-	-	-
<i>Lepomis cyanellus</i> (Green Sunfish)	X	X	-	-	-	-	-	-	-	-	-	-
<i>L. megalotis</i> (Longear Sunfish)	X ⁴	X	-	X	-	-	-	-	-	-	-	-
<i>L. macrochirus</i> (Bluegill)	X	X	-	X	-	-	-	-	-	-	-	-
<i>L. humilis</i> (Redspotted Sunfish)	X ⁴	-	-	-	-	-	-	-	-	-	-	-
<i>Micropterus salmoides</i> (Largemouth Bass)	X	-	-	X	-	-	-	-	-	-	-	-
Percidae (Perches and Darters)												
<i>Etheostoma australe</i> (Conchos Darter) ¹⁶	-	-	-	-	X	-	-	-	-	-	-	-
<i>E. grahami</i> (Rio Grande Darter)	-	X	-	X ^b	-	-	-	-	-	-	-	-
<i>E. lepidum</i> (Green-throat Darter)	-	X	-	-	-	-	-	-	-	-	-	-
<i>E. spectabile</i> (Orange-throat Darter)	X ⁴	-	-	-	-	-	-	-	-	-	-	-
<i>Percina macrolepida</i> (Rio Grande Logperch)	-	X	-	X	-	-	-	-	-	-	-	-
Sciaenidae (Drums and Croakers)												
<i>Aplodinotus grunniens</i> (Freshwater Drum)	X ⁴	X	-	X	-	-	-	-	-	-	-	-
Mugilidae (Mullet)												
<i>Axonostomus monticola</i> (Mountain Mullet)	-	-	-	X ^b	-	X	-	-	-	-	-	-
<i>Mugil cephalus</i> (Striped Mullet)	-	-	-	X ^b	-	X	-	-	-	X	X	-
<i>M. curema</i> (White Mullet)	-	-	-	-	-	X	-	-	-	-	-	-

Species	Plains ¹	Rio Grande basin			Rio Conchos	Guzman Basin ²	Rio Yaqui	Coastal drainages		Death Valley System	Colorado River basin		
		Pecos River ¹	Upper ³	Lower ⁴				Baja California ⁵	Pacific Coast ⁶		Lower ⁷	Gila River	Middle ⁸
Eleotridae (Sleepers)													
<i>Dormitator latrans</i> (Fat Sleeper)	-	-	-	-	-	-	X	-	-	-	-	-	-
<i>Eleotris picta</i> (Spotted Sleeper)	-	-	-	-	-	-	X	-	-	-	X	-	-
<i>Gobiomorus maculatus</i>	-	-	-	-	-	-	X	-	-	-	-	-	-
Gobiidae (Gobys)													
<i>Awaous transandeanus</i>	-	-	-	-	-	-	X	-	-	-	-	-	-
<i>Eucyclogobius newberryi</i> (Tidewater Goby)	-	-	-	-	-	-	-	-	X	-	-	-	-
Cichlidae (Cichlids, Mojarras)													
<i>Cichlasoma beani</i> (Sinaloa Cichlid)	-	-	-	-	-	-	X	-	-	-	-	-	-
<i>C. cyanoguttatum</i> (Rio Grande Perch)	-	X	-	X	-	-	-	-	-	-	-	-	-
<i>Cichlasoma</i> sp.	-	X	-	X	-	-	-	-	-	-	-	-	-
Cottidae (Sculpins)													
<i>Cottus aleuticus</i> (Coastal Sculpin)	-	-	-	-	-	-	-	-	X	-	-	-	-
<i>C. asper</i> (Prickly Sculpin)	-	-	-	-	-	-	-	-	X	-	-	-	-
<i>C. bairdi</i> (Mottled Sculpin)	-	-	-	-	-	-	-	-	-	-	-	-	X ^c
<i>C. gulosus</i> (Rifle Sculpin)	-	-	-	-	-	-	-	-	X	-	-	-	-
<i>Leptocottus armatus</i> (Staghorn Sculpin)	-	-	-	-	-	-	-	-	X	-	-	-	-
Pleuronectidae (Righteye Flounders)													
<i>Platichthys stellatus</i> (Starry Flounder)	-	-	-	-	-	-	-	-	X	-	-	-	-
Soleidae (Soles)													
<i>Trinectes fonsecensis</i>	-	-	-	-	-	-	X	-	-	-	-	-	-

¹Includes representative species of streams flowing into the Mississippi River and directly to the Gulf of Mexico (principally tributaries of the Arkansas and Red rivers); occurrences marked with an "a" are outside the area of present coverage.

²Closed basins (e.g., near Toyahvale, Texas) intimately related to the Pecos River are included.

³Rio Grande mainstream and tributaries (excluding Pecos River, see above) and associated closed basins (e.g., Tularosa Basin) upstream from the inflow of the Rio Conchos (Miller, 1978).

⁴Rio Grande mainstream and tributaries downstream from inflow of the Rio Conchos (Trevino-Robinson, 1959; Hubbs et al., 1977); excluding the formerly-isolated Cuatro Ciénegas Basin (Minckley, 1969; 1978). Occurrences marked with a "b" are outside the area of present coverage.

⁵Rios Carmen, Santa Maria, and Casas Grandes in Mexico, and Mimbres River, New Mexico (Miller, 1978; Hendrickson et al., 1981).

⁶Minor drainages between the Rio Yaqui and the Colorado River delta, draining directly into the Sea of Cortez (Miller, 1959; Follett, 1960).

⁷Minor drainages of western Baja California and southern California and San Diego and Los Angeles drainages, Santa Maria and Santa Inez rivers of the latter area, draining directly into the Pacific Ocean (Follett, 1960; Moyle, 1976).

⁸Includes drainage basins of Mono Lake (originally fishless; Moyle, 1976), Owens, Amargosa, and Mojave rivers (Miller, 1948; Hubbs and Miller, 1948; Soltz and Naiman, 1978).

⁹Includes Laguna Salada, Salton Sea, and distributaries and sloughs on the Colorado River delta (Rio Hardy, New River, Santa Clara Slough, etc.).

¹⁰Mainstream Colorado River (mostly within Grand Canyon), Pluvial White River (including Meadow Valley Wash), Moapa River, Virgin River, minor tributaries to Grand Canyon, and Little Colorado River).

¹¹Defined as upstream from Glen Canyon Dam; occurrences marked with a "c" are outside the area of present coverage.

¹²Numbers of other members of this speciose genus occur in the Arkansas and Red rivers downstream from the area of present coverage, especially in clearer waters of the Ozarkian Province (Metcalf, 1966; Cross, 1967; Pfeiffer, 1975).

¹³Mojave Chub is sometimes considered a full species.

¹⁴Mexican catfishes are poorly understood (Miller, 1976; 1978) and it is likely that more than one species is included here.

¹⁵Restricted to the isolated basin of Pleistocene Lake Otero (Tularosa Basin), New Mexico (Miller and Echelle, 1975).

¹⁶See footnote 12.

Arctic-Boreal Wetlands

Within and adjacent to subalpine forests and grasslands are numerous perennial streams and other aquatic situations bordered by shrub willows (*Salix monticola*, *S. scouleriana*, *S. bebbiana*, *S. lorrata*), and other winter deciduous scrub: e.g., Red Elderberry (*Sambucus racemosa*), Shrubby Cinquefoil (*Potentilla fruticosa*), Goose-berry Currant (*Ribes* spp.), Raspberry (*Rubus* spp.), and at lower boreal and cold temperate elevations, Thin-leaf Alder (*Alnus tenuifolia*) (Fig. 153). While these alpine and subalpine riparian scrublands may be punctuated by Blue Spruce (*Picea pungens*), Aspen (*Populus tremuloides*), and other tree species of the subalpine conifer forest, distinctive riparian tree life forms (and hence riparian forests), are generally absent from this thermal zone.

Except for the highest elevations of the Sangre de Cristo, San Juan, San Pedro, White, and Mogollon mountains, the number and length of subalpine streams in the Southwest is limited by the relatively small watershed areas of sufficient elevation, and also sometimes by geologic situations—e.g., the porosity of respective volcanic and limestone structures of San Francisco Mountains and the Kaibab Plateau in Arizona. Nonetheless, a few informative examples may be found in most mountain ranges approaching or exceeding 3,000 m elevation—including those in southern California (e.g., upper Snow Creek in the San Jacinto Mountains and the upper South Fork of the Santa Ana River in the San Bernardino Mountains). Certain north-flowing streams at lower elevations may also have many characteristics of subalpine systems, such as Workman Creek in the Sierra Ancha of Arizona (1,980 m; Fig. 155).

These boreal scrublands along watercourses are important and distinctive biomes, and in the Southwest provide the southern-most breeding habitats for a characteristic northern avifauna such as Lincoln's Sparrow (*Melospiza lincolni*), White-crowned Sparrow (*Zonotrichia leucophrys*), and MacGillivray's Warbler (*Oporornis tolmiei*). The streams themselves are used as breeding grounds for a few amphibians such as treefrogs (*Hyla* spp.) and also are the past or present home of a number of relicted, native salmonid fishes (e.g., *Salmo clarki*

spp., *S. apache*, *S. gilae*). These trouts are now largely replaced by introduced species such as Rainbow Trout (*S. gairdneri*) and Brook Trout (*Salvelinus fontinalis*).

Many subalpine grassland meadows possess high water tables, so that small marshy ponds or ciénegas are common features. Beaver dams are locally present, and streambanks are frequently marshy where gradients are not too steep. These streamside ciénega habitats support microtine rodents (*Microtus* spp.), Western Jumping Mouse (*Zapus princeps*), and Water Shrew (*Sorex palustris*), among other small mammals. Both Rocky Mountain and Sierran subalpine marshlands are most often vegetated by high-elevation or other cold-climate sedges (*Carex* spp., *Cyperus* spp., *Eleocharis* spp. and *Scirpus* spp.) and rushes (*Juncus* spp. and *Luzula* spp.). Taller life-forms such Roundstem Bulrush (*Scirpus pallidus*) and other aquatics such as mannagrass (*Glyceria* spp., including *G. borealis*) occupy deeper (and hence more permanent) marshes and lakesides (Fig. 154), providing nesting habitat for several species of waterfowl including the Mallard (*Anas platyrhynchos*), and Eared and Pied-billed Grebes (*Podiceps caspicus*, *Podilymbus podiceps*). Denser stands of bulrush also provide nesting habitat for Sora (*Porzana carolina*) and Coot (*Fulica americana*). High altitude amphibians, treefrogs (*Hyla eximia*, *H. regilla*), Cricket Frog (*Pseudacris triseriata*), and Tiger Salamander (*Ambystoma tigrinum nebulosum*), are characteristic of both temporary and permanent ciénega habitats.

Except in the San Juan Mountains, natural lakes are few and greatly outnumbered by small, artificial reservoirs and tanks designed for recreational fishing and livestock use. Although some of these water bodies may be extremely fertile, long periods of snow cover and resulting oxygen depletion in winter, or elevated pH in summer as a result of special chemical and biological conditions, result in only a few providing a substantial fishery for introduced salmonids. They are, however, extensively used by birds and, if fishes are absent, support large numbers of amphibians.



Figure 153. Subalpine riparian scrub along North Fork of the White River, Fort Apache Indian Reservation, Apache County, Arizona. Prevalent species at this locality near the lower limits of subalpine scrub are willows (*Salix bebbiana*, *S. scouleriana*), Thinleaf Alder (*Alnus tenuifolia*), Blueberry Elder (*Sambucus glauca*) and Hawthorn (*Crataegus erythropoda*). Trees along the stream are Blue Spruce (*Picea pungens*), and Engelmann Spruce (*P. engelmannii*), with Ponderosa Pine (*Pinus ponderosa*) upslope above the temperature inversion layer. Elevation ca. 2,400 m.



Figure 154. Subalpine marshland and submergents at Carnero Lake, Apache National-Forest, Apache County, Arizona. The marshland emergent is Mannagrass (*Glyceria borealis*). Elevation ca. 2,750 m.

Cold-Temperate Wetlands

Riparian and other wetland communities in the montane, Plains, and Great Basin biotic provinces of the Southwest are characterized by winter-deciduous trees as well as shrubs and aquatic plants. These ecosystems, while often structurally diverse, are of relatively simple species composition when compared to some riparian communities in warm-temperate and subtropical climates. Adapted to spring flooding after snowmelt, the riparian associations typically are in a successional stage to deciduous forest unless arrested or eliminated by impacts of upstream impoundments and/or grazing by livestock. A large proportion of the Southwest's "live" streams are in this climatic zone (see e.g. Brown et al., 1978). Unlike rivers of moister zones that increase in size and volume throughout the

year in a downstream direction, southwestern rivers flowing from mountains across deserts often have diminution of discharge both up- and downstream from intermediate elevations. Moderate to smaller streams now hold the most diverse native fauna, principally because of habitat diversity provided by channels intermediate between highly erosive, montane regions and aggrading conditions of lowland rivers. In the arid Southwest, such places also allow the greatest degree of permanence because of alternating bedrock and alluvial fill, the former inducing scour of pools and other deep places, and the latter providing shallow, high nutrient, productive reaches in periods of sustained flow.

Montane Riparian Wetlands

In montane regions of the Rocky Mountains and in the highest parts of the Sierra Madre Occidental, a "canyon bottom forest" [Fig. 155] may occur along perennial and near-perennial streams from ca. 2,100-2,300 m down to ca. 1,700 m, and locally to as low as 1,350 m. Narrowleaf Cottonwood (*Populus angustifolia*), maple (*Acer grandidentatum*), Box Elder (*Acer negundo*), alder (*Alnus oblongifolia*) and willows (*Salix* spp.) form a riparian series, in which the trees, shrubs, and grasses of adjacent montane coniferous forest are lesser [yet common] participants (e.g., *Quercus gambelii*, *Pinus ponderosa*, *Abies concolor*, *Populus tremuloides*, *Robinia neomexicana*, *Rhus glabra*, *Blepharoneuron tricholepsis*, etc.). Any of several other riparian short-statured or scrub trees such as Water Birch (*Betula occidentalis*), Rocky Mountain Maple (*Acer glabrum*), American Plum (*Prunus americana*), and Bitter Cherry (*Prunus emarginata*) may be locally important. The vine, Virginia Creeper (*Parthenocissus vitacea*), can add a dash of scarlet to an already colorful autumn woods. An analogous series of Black Cottonwood (*Populus trichocarpa*), White Alder (*Alnus rhombifolia*), Bigleaf Maple (*Acer macrophyllum*), and willow (*Salix scouleriana*) finds limited representation along montane streams in some higher Southern California mountains [*Sierran riparian deciduous forest*].

The dominant aspect of many of these montane stream-sides, however, is often one of shrubbery (= scrubland). This may be a result of the singular presence of younger age classes of riparian trees and/or the heavy and sometimes exclusive representation of one or several shrub willows (*Salix irrorata*, *S. lasiolepis*, etc.). Other riparian scrub species such as Blueberry Elder (*Sambucus glauca*), Red-osier Dogwood (*Cornus stolonifera*), Thin-leaf Alder (*Alnus tenuifolia*), or hawthorn (*Crataegus* spp.) may complement or essentially replace the willows.

The Beaver (*Castor canadensis*) is perhaps the best known montane riparian resident, and Raccoon (*Procyon lotor*) commonly finds its upper elevational limits here. In wider parts of canyons with streamside stands of sedge-grass ciénega, microtine rodents (*Microtus* spp.) often are common. Some of the more densely wooded stream-sides within Rocky Mountain and Madrean conifer forests are important to the distribution of White-tailed Deer (*Odocoileus virginianus*) and Wild Turkey (*Meleagris gallopavo*). The Water Ouzel or Dipper (*Cinclus mexicanus*) is a most characteristic nesting bird. Bleak in winter, these habitats are important in other seasons to a number of colorful migratory songbirds such as the Lazuli Bunting (*Passerina amoena*), Yellow Warbler (*Dendroica petechia*), Black-headed Grosbeak (*Pheucticus melanocephalus*), and Yellow-breasted Chat (*Icteria virens*). Other characteristic birds are the Broad-tailed Hummingbird (*Selasphorus platycercus*), Belted Kingfisher (*Megaceryle alcyon*), Warbling Vireo (*Vireo gilvus*) and Western Flycatcher (*Empidonax difficilis*).

A list of indicative or well represented montane reptiles would include the garter snakes (*Thamnophis elegans*, *T. couchi*, *T. cyrtopsis*, *T. eques*), the Narrow-headed Garter Snake (*T. rufipunctatus*), and Alligator Lizard (*Gerrhonotus kingi*). Amphibians may be represented in the appropriate mountains by either of several treefrogs (*Hyla arenicolor*, *H. regilla*, *H. eximia*) and in California by the mountain Yellow-legged Frog (*Rana mucosa*). Salamanders are the Tiger Salamander in the north, and the Tarahumara Salamander



Figure 155. Rocky Mountain montane riparian forest. "Canyon bottom" habitat along Workman Creek in the Sierra Ancha Experimental Forest, Sierra Ancha Mountains, Gila County, Arizona. Deciduous trees are mostly Big-tooth Maple (*Acer grandidentatum*), Arizona Alder (*Alnus oblongifolia*), Narrow-leaf Cottonwood (*Populus angustifolia*) and Gambel Oak (*Quercus gambelii*). Ponderosa Pine (*Pinus ponderosa*) and White Fir (*Abies concolor*) are prevalent conifers from the adjacent coniferous forest. The shrub-vine Canyon Grape (*Vitis arizonica*) is an important participant in forest openings. Elevation ca. 1,950 m.

(*Ambystoma rosaceum*) in the Sierra Madre Occidental of northwestern México.

Waters of this zone are inhabited by relatively few species of "cold water" fishes. Prior to widespread introductions of Rainbow Trout, most montane streams above 1,800 m were populated by locally endemic species of trouts such as *Salmo apache* in Arizona, *S. gilae* in Arizona and New Mexico, and in the cold-temperate segments of the Sierra Madre Occidental in Mexico, one or more yet-to-be-described species of *Salmo* and the Mexican Golden Trout (*S. chrysogaster*). Many of these native populations are now reduced or extirpated through hybridization with *S. gairdneri* and predation/competition interactions by other introduced salmonids

(Rinne et al., 1981). Another widely introduced species, the European Brown Trout (*Salmo trutta*), descends to somewhat lower elevations where it may be accompanied by the local species of mountain-sucker [genus *Pantosteus*] and such suckers of the genus *Catostomus* that are appropriate to the watershed. Minnows such as spinedace [*Lepidomeda* spp.] and Speckled Dace [*Rhinichthys osculus*] are in the Colorado River basin, and Longnose Dace (*R. cataractae*) occurs in the Rio Grande system. Introduced fishes other than trouts are relatively uncommon in our higher elevation waters, with the exception of the Golden Shiner [*Notemigonus crysoleucus*] in Arizona (Minckley, 1973), which has created substantial management problems by overpopulating fishing lakes.

Plains and Great Basin Riparian Wetlands



Figure 156. Cottonwood [*Populus deltoides* ssp. *sargentii*] forest along the Cimarron River near the Colorado-New Mexico-Oklahoma boundaries. It is December and this deciduous flood plain forest, although appearing bleak and uninviting, is actually a haven for wildlife during the wind swept storms of winter.

Monotypic gallery forests and woodlands of Plains Cottonwood (*Populus deltoides* ssp. *sargentii*), Rio Grande Cottonwood (*P. wislizenii*), Peachleaf Willow (*Salix amygdaloides*), or Narrowleaf Cottonwood are the dominant climax vegetation along streamsidelines east of the Rocky Mountain and in much of the Great Basin (Figs. 156, 157). Most riparian reaches are in successional stages, and scrublands interrupted by an occasional cottonwood grove or tree and composed chiefly of scrub willows (*Salix exigua* and others; Fig. 158), or less commonly, scrubby trees such as Red-osier Dogwood, are typical riparian communities.

In the western, warmer portions of the Great Basin biotic province, disclimax riparian scrublands and strands populated by the introduced Saltcedar (*Tamarix chinensis*) now comprise many miles of river and stream channels, including ephemeral tributaries (Fig. 159). This situation is especially prevalent in areas of manipulated discharge below storage reservoirs, as along the San Juan River near Farmington, New Mexico. Other exotic plants such as Russian Olive [*Elaeagnus angustifolia*] and Camelthorn (*Alhagi camelorum*) have become naturalized and contribute increasingly to the composition of scrublands along these and other Great Basin drainages.

Although these environments are important to a number of riparian animal species of more general distribution (e.g., Yellow-breasted Chat), at least one bird, the Black-billed Magpie (*Pica pica*), is centered here. Also, several species of the Eastern deciduous forest find their southwestern limits in local associations of Plains and Great Basin riparian communities. These include Catbird (*Dumetella carolinensis*), American Redstart (*Setophaga ruticilla*), Veery (*Catharus fuscescens*), Eastern Phoebe (*Sayornis phoebe*), and Red-headed Woodpecker (*Melanerpes erythrocephalus*). Woodhouse's Toad (*Bufo woodhousei*), spadefoot toads [*Scaphiopus intermontanus*, *S. bombifrons*, *S. hammondi*], Leopard Frogs (*Rana pipiens* complex), and garter snakes (*Thamnophis radix*) are amphibians and reptiles well represented in these riparian environments.

Of the piedmont and alluvial rivers with cold temperate waters, only those draining to the Gulf of Mexico have relatively diversified fish faunas (Table 32). The largest southwestern ichthyofauna is that of the Plains rivers and of the Rio Grande system. The upper portion of Plains streams, e.g., the uppermost Red River system (Fig. 146), supports numerous minnows characteristic of smaller or moderate-sized habitats: Plains Stoneroller (*Campostoma anomalum*), Creek Chub (*Semotilus atromaculatus*), Plains Minnow [*Hybognathus placitus*], Flathead Chub (*Platygobio gracilis*), Sand Shiner (*Notropis stramineus*), Fathead Minnow [*Pimephales promelas*], and others. White Sucker (*Catostomus commersoni*) also is common, and has been introduced into some western drainages. Plains Killifish (*Fundulus kansae*) lives in shallow, saline, more severe places. An infusion of Plains species occurred into the Rio Grande basin as the Pecos River cut northward through unconsolidated sediments along the southeastern flank of the Rocky Mountains and pirated headwaters of the Brazos, Colorado (of Texas), and Canadian rivers (Belcher, 1975; Leonard and Frye, 1975). Likely examples of this event are Sand Shiner, Flathead, and Creek chubs, and such pairs as Plains and Rio Grande killifishes (*Fundulus kansae* and *F. zebrinus*) and Red River and Pecos pupfishes [*Cyprinodon rubrofluviatilis* and *C. pecosensis*; Echelle and Echelle, 1978]. Remnants of an "old" (Tertiary) fauna also



Figure 157. A "linear" forest of Narrow-leaf Cottonwood [*Populus angustifolia*] along irrigation ditches near Springerville, Apache County, Arizona. Note the scrub understory that is an important cover-type for wildlife during the cold of winter. Elevation ca. 2,150 m.

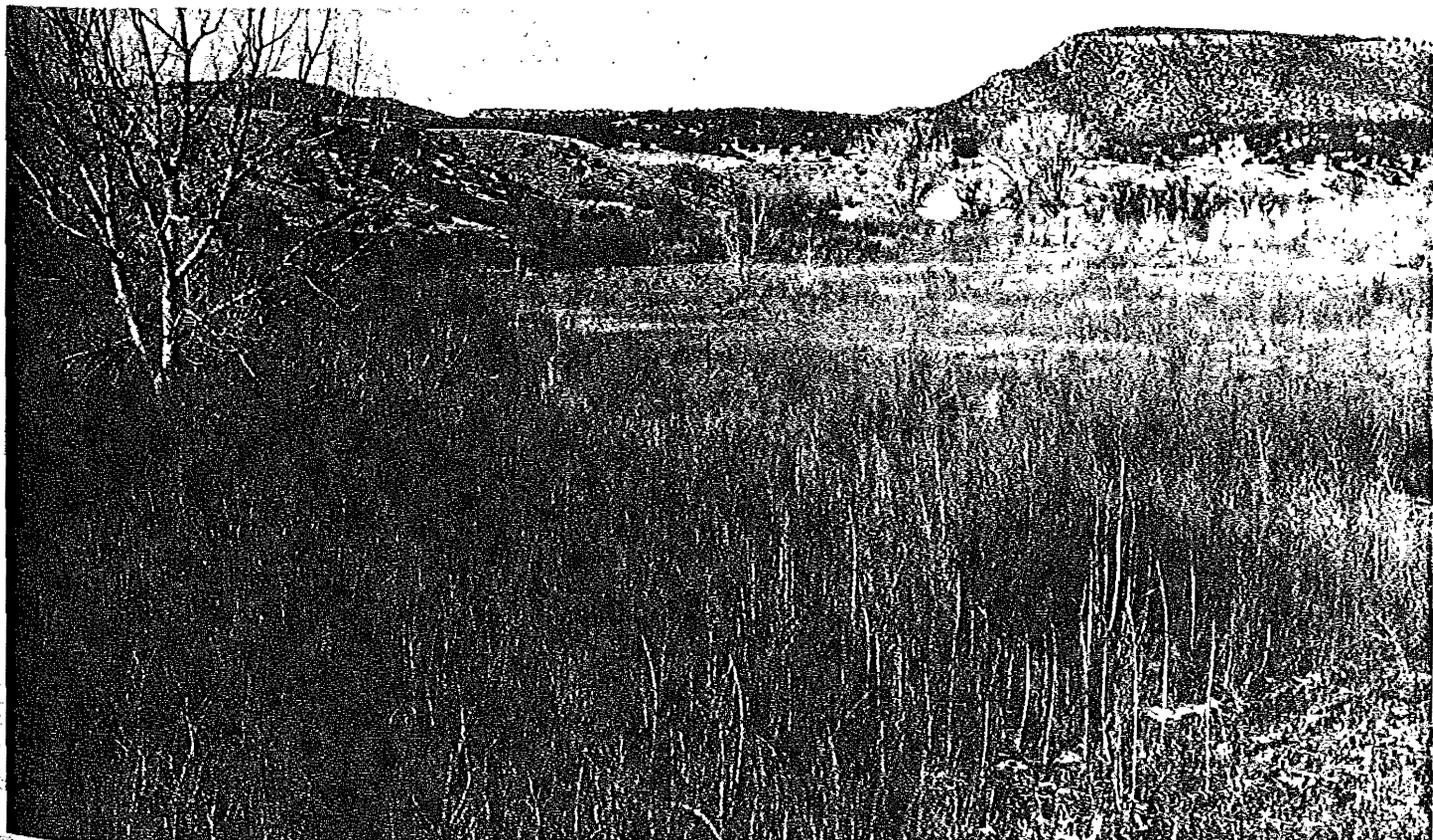


Figure 158. Successional scrubland of scrub willows [*Salix* spp.] and young cottonwood (*Populus sargentii*) along the Vermejo River. Colfax County, New Mexico. Given time these communities will pass into forest and woodland - unless, and until, interrupted by high intensity flooding. Elevation ca. 1,800 m.

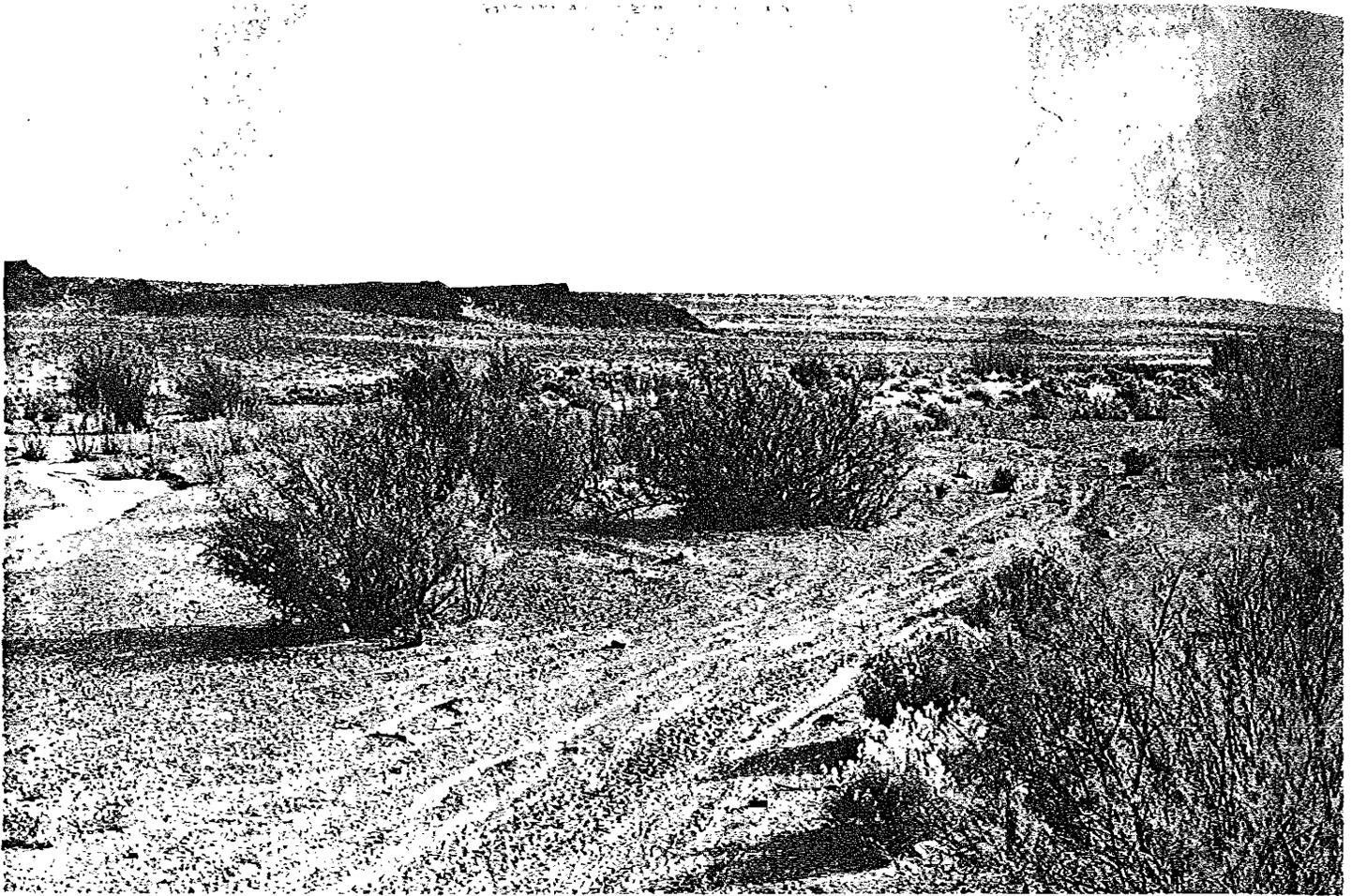


Figure 159. Great Basin riparian strand along Hamblin Wash, Coconino County, Arizona. An open stand of Saltcedar (*Tamarix chinensis*) and smaller shrubs on the floodplain of an ephemeral stream (dry wash) within the Great Basin Desert. Elevation ca. 1,500 m.

persist in the upper Rio Grande basin, e.g., Pecos Chub (*Gila pandora*) and a mountain-sucker (*Pantosteus plebeius*).

The Colorado River system physically dominates the Southwest and hosts an impressive array of endemic genera and species of fishes. Tributaries to the middle Colorado River now range from series of springs rising from the intermittent channel of Pluvial White River and Meadow Valley Wash in southern Nevada [Hubbs and Miller, 1948; LaRivers, 1962], to larger streams with local perennial flow such as the Virgin and Little Colorado rivers. Extreme isolation has led to differentiation. Each major stream has its own species or subspecies of spinedace: *Lepidomeda vittata* in the Little Colorado, *L. mollispinis mollispinis* in the Virgin River, *L. mollispinis pratensis* in Meadow Valley Wash, *L. altivelis* in lower White River, and *L. albivallis* in the isolated

upper White River (Miller and Hubbs, 1960). Mountain-suckers, although all referred to *Pantosteus clarki* by Smith (1966), show similar differentiation (Minckley, 1973), as do local populations of chubs (*Gila robusta jordani* in the White River system and *G. robusta seminuda* in the Virgin River) and Speckled Dace (Williams, 1978). Thermal endemics of the Moapa River (the springfish, *Crenichthys baileyi*), and Moapa Dace [*Moapa coriacea*] will be discussed later under springs and marshlands, although the last is characteristic of both pools and relatively swift runs.

The upper Colorado River system, mostly north of our area of coverage, supports special big-river fishes to be covered below, plus Roundtail Chub (*G. robusta robusta*), Speckled Dace, and tributary forms of Blue-head Mountain Sucker (*Pantosteus discobolus*).

Montane, Plains and Great Basin Marshlands

Marshes, nowhere extensive in the Southwest, occupy only a small area in this climatic zone so that their wildlife values are particularly high. Some larger, natural examples include Mormon and Stoneman lakes in Arizona, and Buford (Stinking), Boulder, and Horse lakes in New Mexico. Other sizable areas of natural and "managed" marshlands occur near Las Vegas, New Mexico (e.g., on Monte Vista and Alamosa National Wildlife refuges). Smaller examples are clustered in poorly-drained portions of the Mogollon Rim in Arizona, especially where sinkholes have developed through subsurface solution, and occasionally elsewhere within montane forests as well as in the Plains and Great Basin [Fig. 160; Wright, 1964; Wright and Bent, 1968].

Marsh vegetation is characteristically "zoned" along a littoral gradient. Depending upon seasonal water depth, water chemistry, time and "chance," it may be composed largely of emergent plants such as cattail (*Typha latifolia*), bulrush or tule (*Scirpus acutus*), rushes (*Juncus* spp.), sedges (*Carex* spp.), Three-square [*Scirpus americanus*], Salt Grass (*Distichlis stricta*), etc., or be mostly submergent, e.g., series of Water Milfoil (*Myriophyllum spicatum*), pondweeds (*Potamogeton* spp.), introduced water-weed (*Elodea* spp.), manna grasses (*Glyceria* spp.), or charophytes [*Chara* spp., *Nitella* spp.]. Often there is some interspersed with trees and shrubs, particularly willows. Spike-rushes (*Eleocharis* spp.) are characteristic emergents in marshes subject to desiccation, and often occur there in monospecific stands [Figs. 161, 162].

These marshlands provide feeding and watering habitat for a number of migratory bats. Muskrats [*Ondatra zibethicus*] may be common all year. The Western Jumping Mouse is best represented in interior marshes, while Mink [*Mustela vison*] is rare, and apparently restricted in the Southwest to a few wetlands in and near the Sangre de Cristo Mountains.

Almost all cold-temperate marshlands host some nesting as well as migrating waterfowl. The principal species are Mallard, Pintail [*Anas acuta*], Cinnamon Teal [*A. cyanoptera*], Redhead [*Aythya americana*], and Ruddy Duck (*Oxyura jamaicensis*). Although no longer a nesting bird in the Southwest, the Sandhill Crane (*Grus canadensis*) still relies heavily on several of those areas for staging sites during migration. The short-statured and more open plant associations are used by cranes, waterfowl, and numerous shorebirds, and the taller structured emergents such as bulrushes (*Scirpus americanus*, *S. acutus*, etc.) may provide nesting sites for American Bittern [*Botaurus lentiginosus*], Virginia Rail [*Rallus limicola*], Sora, Common Yellow Throat (*Geothlypis trichas*), Yellow-headed Blackbird [*Xanthocephalus xanthocephalus*], Red-winged Blackbird (*Agelaius phoeniceus*), and Long-billed Marsh Wren [*Cistothorus palustris*].

Western Garter Snake is the most commonly encountered reptile, and Leopard Frogs (*Rana pipiens* complex) and Tiger Salamander are amphibians found throughout the region. Cricket Frogs, although indicative, are local in distribution.

Fishes are rarely present in these habitats, other than the young of minnows and suckers that are seasonally present in marshy areas adjacent to streams. Marshlands with open water have been stocked with numerous exotics, however, including salmonids for seasonal fisheries. Others include eastern centrarchids and cyprinids, many of which are now



Figure 160. Montane (Rocky Mountain) marshland of waterweed [*Sagittaria* spp.], a widespread, cold temperate taxon, at Mormon Lake, Coconino National Forest, Coconino County, Arizona. Elevation ca. 2,150 m.



Figure 161. Montane marshland of Spikerush (*Eleocharis parvula*) at Sunflower Flat, Kaibab National Forest, Coconino County, Arizona. A seasonally flooded environment that provides waterfowl nesting habitat on an interim basis. Elevation ca. 2,150 m.



Figure 162. Interior marsh within Great Basin desert scrub. Except for small patches of Saltcedar (*Tamarix chinensis*; dark group in left center background), Saltgrass [*Distichlis stricta*] almost exclusively dominated this now-drained wetland (Obed Meadows) south of Saint Johns, Apache County, Arizona. Elevation ca. 2,000 m. This cosmopolitan halophyte constitutes the principal vegetation of many alkali wetlands in the Southwest from sea level to more than 2,150 m.

considered noxious; e.g., Green Sunfish [*Lepomis cyanellus*] and Golden Shiner, and predators such as Northern Pike [*Esox lucius*]. The last species may exert pressure on young of

nesting waterfowl, and will certainly have an undesirable impact on other native aquatic animals if it becomes established in streams.

Warm-Temperate Wetlands

Included in this climatic zone are some of the Southwest's most extensive, and yet more endangered wetlands. Ranging from open mud flats to complex broad-leaf deciduous forests with canopies more than 30 m above the ground, these habitats provide a wide diversity to an enormous variety of aquatic and semi-aquatic inhabitants.

Biotic communities represented include several fasciations of riparian deciduous forest, riparian scrub, and both interior and coastal marshes and strands (Fig. 163). Also present, but outside the scope of this discussion, are an as-yet-undetermined number of inland and marine submergent communities. Moreover, these last biomes with their complex plant and animal reefs, kelp "forests," eelgrass "meadows," and a myriad of other underseascapes, support at least seasonally a more or less pelagic mammalian fauna of Gray Whale (*Eschrichtius robustus*), Harbor Porpoise (*Phocoena vomerina*), dolphins (*Lagenorhynchus obliquidens*,

Delphinus bairdi, *Tursiops gilli*) and formerly, the Southern Sea Otter (*Enhydra lutris nereis*), as well as providing feeding habitat for numerous oceanic birds.

Marine reptiles are absent or poorly represented in these waters. Reproducing populations of sea turtles and sea snakes generally are restricted to tropic-subtropic waters farther south. The fish fauna in coastal marine habitats is, however, large and diversified. Because of the California current, temperate marine environments extend south along the Pacific Coast to below the 27th Parallel of Baja California (Fitch and Lavenberg, 1975). Waters as far south as Bahía Magdalena (between the 24th and 25th parallels) remain cold enough to form a barrier to tropical coastal fishes. The Golfo de California (Sea of Cortez) is protected from these currents, and has a tropic-subtropic fish fauna clearly derived from the south (Walker, 1960; Thomson et al., 1979).

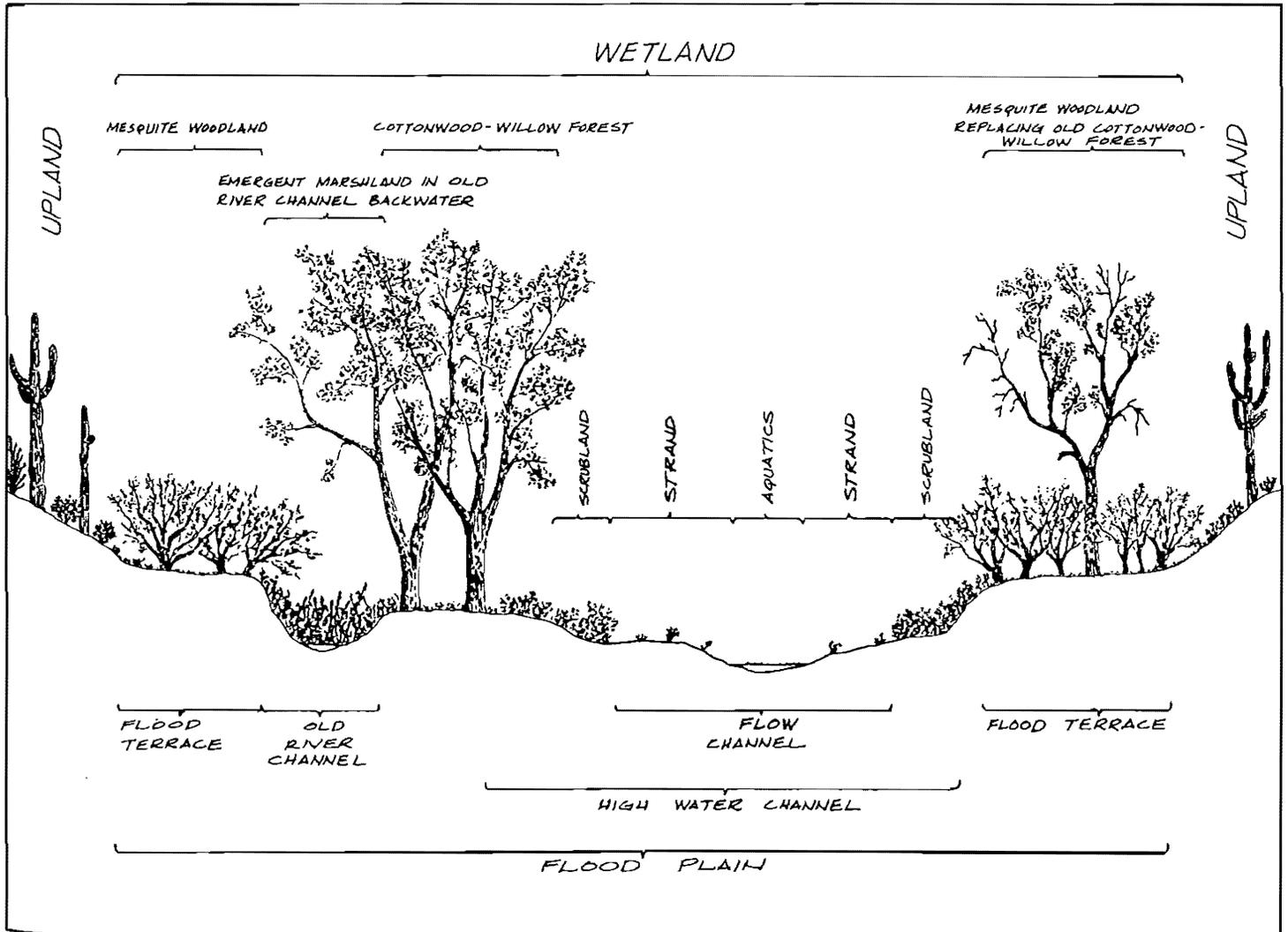


Figure 163. Semi-diagrammatic representation of riparian communities in warm temperate to subtropical habitats of the American Southwest.

Interior and Californian Riparian Deciduous Forests and Woodlands

These winter deciduous communities are diverse, because high altitude species penetrate downslope to occur among lowland forms [Fig. 145]. Originally, they occupied many of the major as well as secondary drainages in the Californian, Mohavian, sub-Mogollon (=Arizonan), Madrean, and Chihuahuan biotic provinces, where they are now greatly reduced because of reductions in stream flow. These communities are maintained along perennial or seasonally intermittent streams and springs, and may be divided into two major vegetation-types (series) — cottonwood-willow and mixed broadleaf.

These are relictual communities. The present distributions of the two major vegetation types, particularly the mixed broadleaf, reflect a contraction of the formerly widespread, Early Tertiary mixed mesophytic forest. These riparian forests are vernaly adapted to Early Tertiary climates and have retreated to pockets where the warm temperate (ancient) climate persists.

Where streamflows are intermittent, well-developed gallery forest can be expected only where surface flow reliably occurs during winter-spring months, because the onset of the spring growing season can be expected prior to April 15 [Zimmerman, 1969; Hibbert et al., 1974]. After mid-April, increased evaporation and phytotranspiration often result in only subsurface flow in all but the larger streams, at least during daytime. The Southwest's warm-temperature riparian forests and woodlands, therefore, require abundant water during March and April when most arboreal species leaf, set seed, and germinate [Zimmerman, 1969]. Summer precipitation usually does not result in sustained streamflow in seasonal stream channels [Zimmerman, 1969; Hibbert, 1971; Hibbert et al., 1974], and riparian forests in the Southwest have therefore remained vernaly adapted. Probably for this reason, these forests are poorly represented and often absent from western pediments of the Sierra Madre Occidental where winter-spring precipitation and runoff is characteristically low.

Communities of cottonwood [*Populus fremontii* and others; in portions of the Chihuahuan biotic province, *P. fremontii* ssp. *mesetae*], and willows [*Salix goodingii*, *S. exigua*, *S. bonplandiana*, and others] are characteristic stream features throughout the Southwest's warm-temperature zones. These short-lived associations are typically encountered and reach their best development in alluvial sands, clays, and gravels on flood plains. The forest canopy may be from 15 to 30 m or more in height and with open and park-like understories in mature groves, or populated by thickets of young cottonwoods or willow depending upon stage and grazing intensity.

Indications are that cottonwood-willow associations are maintained and depend on periodic spring floods [Fig. 164]. Evidence for the winter-spring flood adaptation of these communities are "new" forests along undammed portions of the Verde and San Pedro rivers following spring floods in 1962 and 1967, respectively, a result of fortuitous timing of floods with the narrowly defined germination requirements of these riparian salices. Also, the presence of Californian and Mohavian cottonwood-willow fasciations would indicate that they too are vernaly adapted, and that summer precipitation and runoff is of little or no importance to their regeneration and only encourages competitors such as Saltcedar.

Stabilized flows from storage reservoirs and summer flooding in today's wider channels facilitates dissemination of Salt-

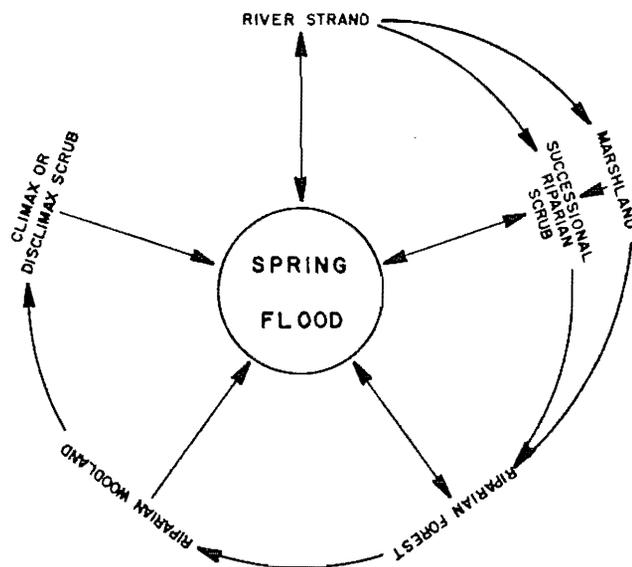


Figure 164. Hypothetical successional cycle of Southwestern riverine wetlands based on and around the natural flooding phenomena of the region.

cedar, allowing that species to complement or replace cottonwood and willow along many miles of the Rio Grande, Pecos, upper Gila, and other rivers where such conditions now occur. Stabilized flow below dams seems especially to result in decadent stands of native trees in which reproduction is lacking. Unlike other riparian trees, such as sycamores (*Platanus* spp.) that reproduce almost entirely by sprouting into clones, cottonwood and willow are mainly disseminated by seed. Studies by Horton et al. [1960] and Zimmerman [1969] have shown that these species germinate in spring, and that seeds remain viable for less than 7 weeks. If receding waters fail to provide a suitable seed bed, little or no reproduction of these short-lived species will occur.

Saltcedar produces seed from March through October in the Southwest, and may colonize seed beds similar to those used by cottonwood and willow (Horton, 1977). Summer flooding therefore, may enhance that species, except in canyon-bound rivers where the violence of scour appears to exclude it (Minckley and Clark, 1979; Turner and Karpiscak, 1980). Wider places in stream channels provide ameliorating effects on such flooding, so that only major channel-straightening events (Burkham, 1972) can remove dense Saltcedar cover and allow germination and successful recolonization by native trees. The advent of extensive water storage with attendant regulation of streamflow and reduction of floods, coupled with invasion of Saltcedar, have resulted in a great reduction of interior cottonwood-willow communities. Intensity of livestock predation along many stream channels adds another factor often alone sufficient to preclude survival of the limited numbers of seedlings.

Mixed broadleaf series of Interior and Californian riparian deciduous forest occur along rubble-bottomed perennial and near-perennial streams. In the interior Southwest (sub-Mogollon Arizona and New Mexico, northwestern Chihuahua and northeastern Sonora; Figs. 165, 166), aboreal constituents may be admixtures of stands of regional species or ecotypes of such Holarctic genera, as Arizona Sycamore (*Platanus wrightii*), Velvet Ash (*Fraxinus pennsylvanica* var. *velutina*), Fremont Cottonwood, Arizona Alder, Arizona Walnut (*Juglans major*) and willows (*Salix exigua* and others). At some of the higher elevations (ca. 1,400 to 1,800 m), Boxelder, Bigtooth Maple, Narrowleaf Cottonwood, and cherries (*Prunus* spp.) may make their appearance and even dominate locally. At lower elevations (1,100 to 1,500 m), a number of trees of more southern distribution are often present: e.g., Western Soapberry (*Sapindus saponaria* var. *drummondii*), Texas Mulberry (*Morus microphylla*), Netleaf Hackberry (*Celtis reticulata*), and Mexican Elder (*Sambucus mexicana*). Arizona Cypress (*Cupressus arizonica*) is not uncommon, and the forest or woodland often contains oaks (*Quercus gambelii*, *Q. emoryi*, *Q. arizonica*) and conifers (*Pinus ponderosa*, *Juniperus deppeana*) from upstream and adjacent uplands. Near settlements and locally elsewhere, such exotic trees as the Tree-of-heaven (*Ailanthus altissima*), Catalpa (*Catalpa bignonioides*), Osage-orange (*Maclura pomifera*), and even fruit trees may be present. Some of the more noticeable understory species include Bracken Fern (*Pteridium aquilinum*), Smooth Sumac (*Rhus glabra*), Poison-ivy (*Rhus toxicodendron*) and several deciduous vines, especially Canyon Grape (*Vitis arizonica*).

Californian mixed broadleaf forests and woodlands (Figs. 167, 168) have much the same appearance and share many of the same species and genera as their interior counterparts.

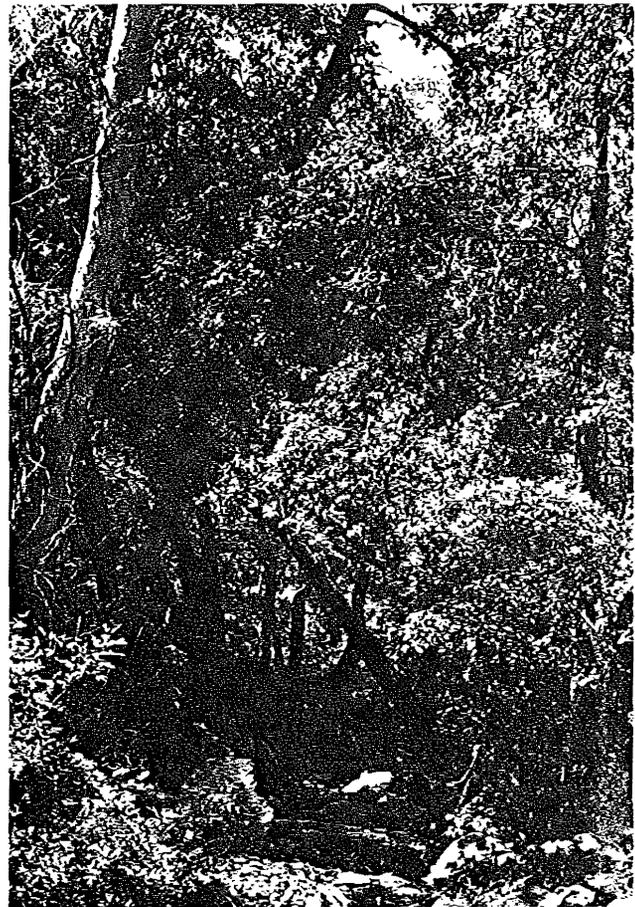


Figure 165. Summer aspect of Interior riparian deciduous forest (mixed broadleaf series) along Gap Creek, Yavapai County, Arizona. A "gallery" forest of the interior riparian "big six"—sycamore (*Platanus wrightii*), alder (*Alnus oblongifolia*), willows (*Salix gooddingii*, *S. bonplandiana*), walnut (*Juglans major*), ash (*Fraxinus pennsylvanica* var. *velutina*), cottonwood (*Populus fremontii*)—and other winter deciduous trees along a boulder-bottomed, perennial stream. Elevation ca. 1,200 m.

While the sycamore and alder here are *Platanus racemosa* and *Alnus rhombifolia*, the widespread *Populus fremontii*, *Fraxinus pennsylvanica* var. *velutina*, *Sambucus mexicana*, *Salix gooddingii*, and *Salix nigra* are represented in both fasciations. Canyon Live Oak (*Quercus chrysolepis*) and Coast Live Oak (*Q. agrifolia*) are often important arboreal constituents and Poison Oak (*Rhus toxicodendron*) is an important understory component in southern California and northern Baja California del Norte riparian communities, as is California Blackberry (*Rubus vitifolius*).

As in cottonwood-willow associations, lowered streamflow has reduced a number of mixed broadleaved forests and woodlands to scattered individual trees, opening the canopy and reducing its desirability for some species of wildlife. Because of previous watershed practices, flash flooding of a destructive nature now too often destroys many miles of these streamside forests. Timbering practices and grazing by livestock has further reduced and affected the forest understory by curtailing or eliminating some forest-associated species.



Figure 166. Mature broadleaf series of Interior riparian deciduous forest along Cajón Bonito, northern Sonora, Mexico. Species present are the same as for Gap Creek (excluding alder; Fig. 165). Elevation ca. 1,100 m; photograph by Dean A. Hendrickson, June, 1978.

Numerous wildlife species are totally or largely dependent on these riparian deciduous communities and many others reach their greatest densities there. Two tree squirrels, Arizona Gray Squirrel (*Sciurus arizonensis*) and Apache Fox Squirrel (*S. nayaritensis*), are largely confined to mixed broadleaf forests within their respective Mogollon and Madrean provinces. The Western Gray Squirrel (*S. griseus*) and introduced Fox Squirrel (*S. niger*) use analogous broadleaf forests in California. Now extremely rare, the River Otter (*Lutra canadensis*) was at one time found in the interior Southwest within warm temperate streams. This species, like the beaver, is more a stream obligate than in need of forest per se.

Other tree-requiring species found in riparian deciduous forests are the Raccoon, and, in California, the introduced Opossum (*Didelphis marsupialis*). Cliffs typically associated with warm temperate canyon streams support small carnivores such as the Ringtailed Cat (*Bassariscus astutus*) and skunks (*Mephitis* spp., *Spilogale putorius*). In drier places, burrowing mammals such as pocket gophers (*Thomomys* spp.) may also be largely restricted to this mesic zone. Numerous bats roost in riparian trees [e.g., Red Bat, *Lasiurus borealis*], or in crevices and holes in cliffs (*Myotis* spp., *Pipistrellus hesperus*), preying on the rich aquatic and riparian insect fauna.

Several nesting birds are obligate to either riparian deciduous trees, cliffs, or the streams themselves. Warm-temperate-inhabiting examples in the interior Southwest include Summer Tanager (*Piranga rubra*), Mississippi Kite (*Ictinia mississippiensis*), Zone-tailed Hawk (*Buteo albonotatus*), and Black Hawk (*Buteogallus anthracinus*); the White-tailed Kite (*Elanus leucurus*) nests in Californian riparian deciduous forest, while the Yellow Warbler, Yellow-billed Cuckoo (*Coccyzus americanus*), Bullock's Oriole (*Icterus bullocki*), and numerous other insectivores such as the Cliff Swallow (*Petrochelidon pyrrhonota*) are common to both biomes. Many others are well represented, and the Madrean fasciations often are host to several neotropical raptors, numerous hummingbirds, [i.e., Blue-throated (*Lampornis clemenciae*), Violet-crowned (*Amazilia verticalis*), Lucifer (*Calothorax lucifer*) and Broad-billed (*Cyananthus latirostris*)], and songbirds e.g., Sulphur-bellied Flycatcher (*Myiodynastes luteiventris*), Rose-throated Becard (*Platypsaris aglaiae*), and Coppery-tailed Trogon (*Trogon elegans*). These last and some sub-Mogollon communities also provide important habitats for common game species, as the White-tailed Deer, Black Bear (*Ursus americanus*), and Wild Turkey, also found in Eastern deciduous forests.

Riparian deciduous forests and stream channels are of equal importance to cold-blooded life forms, including the

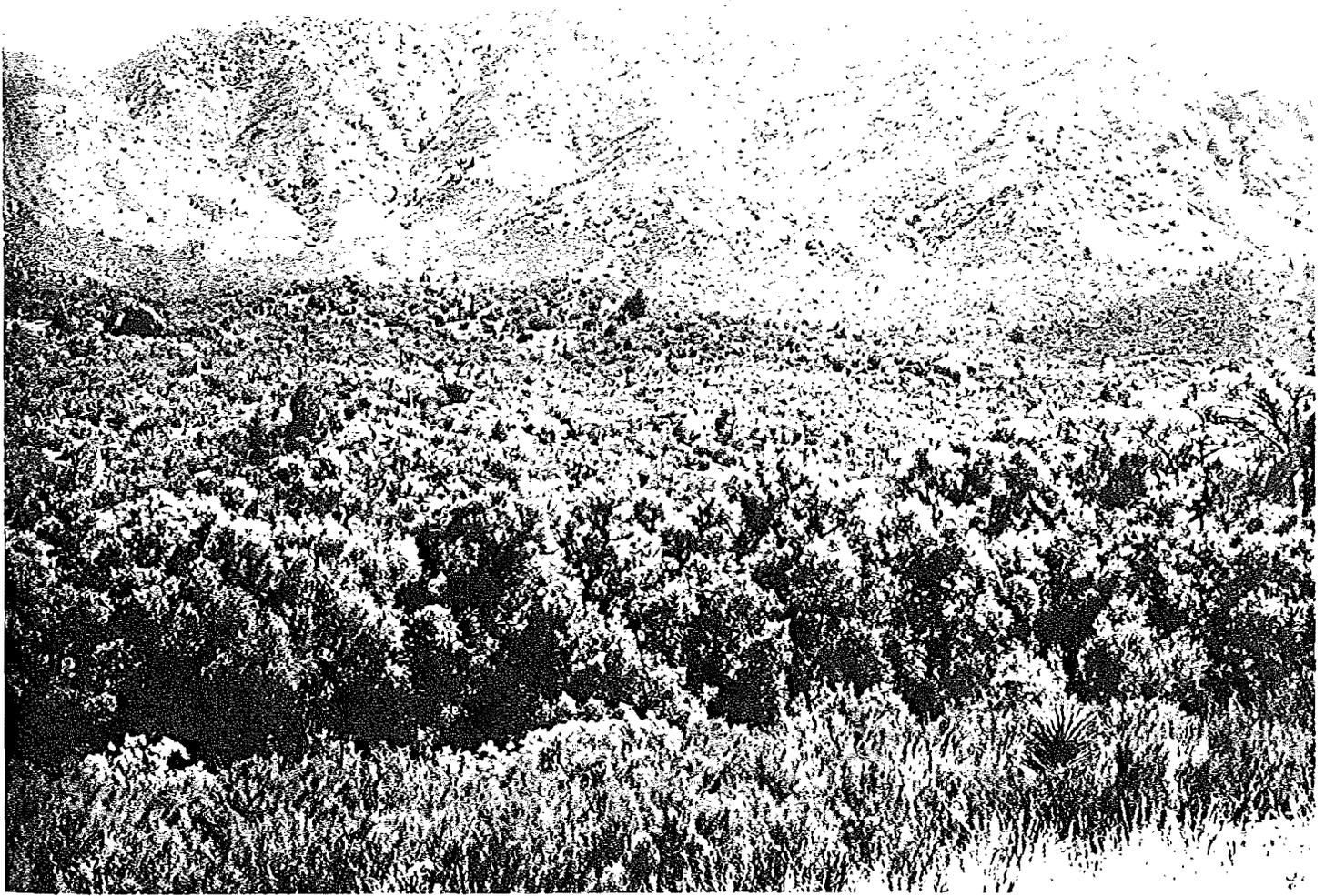


Figure 167. Exterior view of Californian riparian deciduous forest (*Platanus racemosa*, *Salix gooddingii* series) along Arroyo San Rafael, Baja California del Norte, Mexico. The change in life-form height between this linear wetland community and the adjacent upland chaparral is readily apparent. Note the extensive but discontinuous areas of coastal scrub on hillsides, which are subclimax here to chaparral and the result of recent fires. Elevation ca. 1,350 m.

California Newt (*Taricha torosa*), Ensatina (*Ensatina eschscholtzi*), Pacific and California Slender Salamanders (*Batrachoseps pacificus*, *B. attenuatus*), and California Toad (*Bufo boreas holophilus*). Also present are the arboreal or boulder-inhabiting Pacific Treefrog and California Treefrog (*H. cadaverina*); Canyon Treefrog and Arizona Treefrog (*H. wrightorum*) are in the interior. Species of the *Rana pipiens* complex also are common in the interior, and in Mexico the Tarahumara Frog (*Rana tarahumarae*) and stream-adapted Tarahumara Salamander (Collins, 1979) are present at warm-temperate elevations.

Leaf litter along streams may provide habitat for alligator lizards, *Gerhonotus multicarinatus* in California and *G. kingi* in the interior. Where suitable loose soils are present along Californian streams one may find the California Legless Lizard (*Anniella pulchra*). Numerous snakes such as king-snakes (*Lampropeltis* spp.) are well represented in streamside environments, and some, such as Ringnecked Snake (*Diadophis punctatus*), are most often found within riparian forest and woodland. In Madrean fasciations one may encounter the Green Rat Snake (*Elaphe triaspis*), Vine Snake (*Oxybelis aeneus*), and Huachuca Blackhead Snake (*Tantilla wilcoxi*).

wilcoxi). Streams provide hunting grounds and escape areas for several species of the more or less aquatic garter snakes, depending on biotic province and microhabitat characteristics.

As noted before, diversity in fishes is high at intermediate elevations in warm temperate habitats. Most characteristic in the Gila River Basin are Roundtail Chub, Longfin Dace (*Agosia chrysogaster*), Sonoran Sucker (*Catostomus insignis*), and Desert Mountain-sucker (*Pantosteus clarki*). Spikedace (*Meda fulgida*) and Loach Minnow (*Tiaroga cobitis*), each a member of a monotypic genus endemic to the Gila River, may also occur, as may Speckled Dace in cooler, well-shaded streams or in large rivers at intermediate elevations. This same assemblage, less the two Gila River endemics, also is present in the Bill Williams River, tributary to the lower Colorado River mainstream.

The north-flowing Río Conchos, originating in the rugged and inaccessible Sierra Madre Occidental of western Mexico, is occupied by a few fishes of Plains origins, e.g., Longnose Dace (*Rhinichthys cataractae*) and Fathead Minnow. However, Mexican Stoneroller (*Campostoma ornatum*) replaces Plains Stoneroller, and Mexican species with little relationships to the north are dominant, e.g., Chihuahuan Shiner (*Notropis*

chihuahuana), Ornate Minnow (*Codomu ornata*), and others (Table 32). The influence of the Plains fauna in the Río Conchos drainage diminishes rapidly to the West, as does overall faunal diversity. The fathead minnow is native to the basin of Lago de Guzmán. The Beautiful Shiner (*Notropis formosus*) found there is a close relative of the Red Shiner. All other species are of the "old" fauna, e.g., Chihuahuana Chub (*Gila nigrescens*) and a mountain-sucker (*Pantosteus plebeius*), or are of Mexican origins.

The Río Yaqui watershed is a composite of sub-basins derived from the Río Casas Grandes, Río Conchos, Gila River, and drainages to the south and west (Hendrickson et al., 1981). Colorado River fishes such as Roundtail Chub appear here, but species characteristic of north-central Mexico, Ornate Minnow, Mexican Stoneroller, Mesa del Norte Chub (*Gila pulchra*), etc., mostly prevail. The coarse-scaled Yaqui Sucker (*Catostomus bernardini*) occurs from mountains through deserts, and is scarcely separable from the Conchos Sucker (*C. conchos*) to the east or the Sonoran Sucker (*C. insignis*) of the Gila River basin to the north (Miller 1976). The Longfin Dace, a minnow adapted to severe conditions of the Sonoran Desert (Minckley and Barber, 1971), but also moving into tropical and temperate habitats, also is shared by the Río Yaqui and Gila River, as is the Sonoran Topminnow (*Poeciliopsis occidentalis*).

To the west, coastal drainages of southern California have few native fishes, and those that persist are under severe pressure from human population growth and use of existing water. The omnipresent Speckled Dace occurs there along with Arroyo Chub (*Gila orcutti*) and Santa Ana Mountain-sucker (*Pantosteus santaanae*) in tributaries to the Los Angeles Basin, implying by their presence a former connection of that drainage with the Colorado River system (Smith, 1966). The only native fishes to occupy all coastal drainages in southern California are those able to disperse through sea water, e.g., Threespine Stickleback (*Gasterosteus aculeatus*) and California Killifish (*Fundulus parvipinnis*) (Moyle, 1976). In the interior, the Death Valley system contains only remnants of fluvial fishes persisting in springs and marshes connected by short reaches of flowing water; these relicts of wetter times are discussed later.

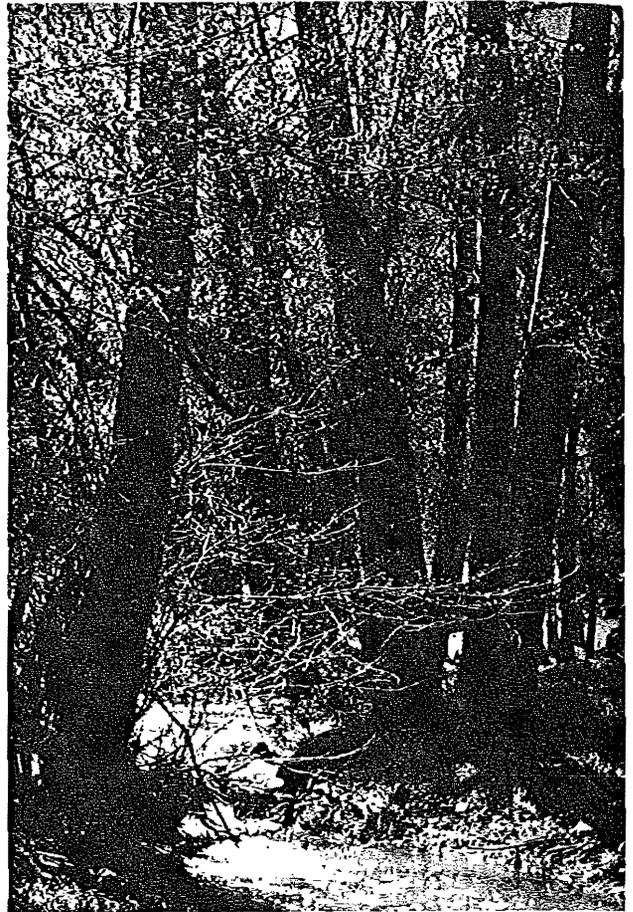


Figure 168. Interior view of Californian riparian deciduous forest (mixed broadleaf series) of alder (*Alnus rhombifolia*) along South Fork of San Felipe Creek, San Diego County, California. It is early spring and the alders are just leafing out; immediately downstream was a mixture of such typical Californian riparian species as sycamore (*Platanus racemosa*), cottonwood (*Populus fremontii*), willow (*Salix gooddingii*) and Canyon Live Oak (*Quercus chrysolepis*) Elevation ca. 1,375 m.

Riparian Scrublands

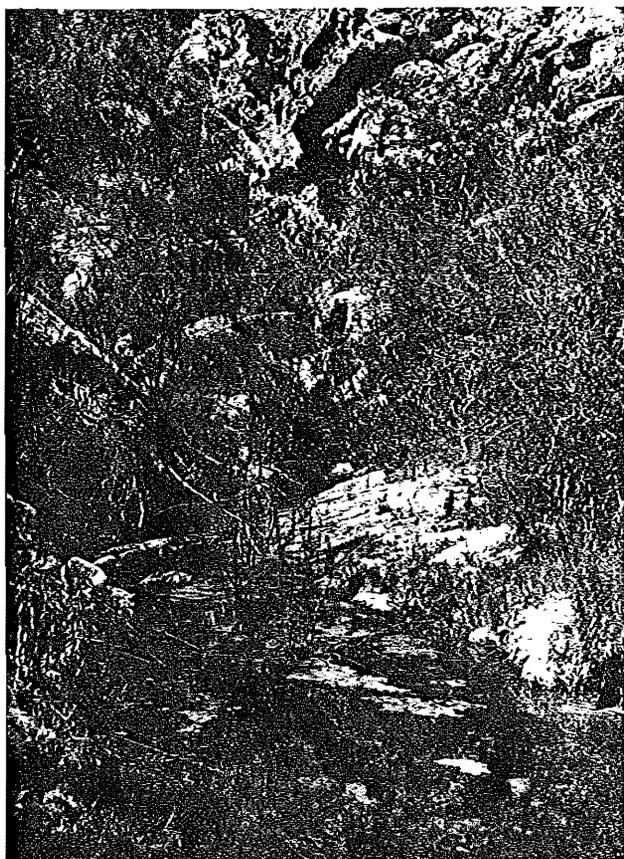


Figure 169. Diverse riparian scrubland in Grapevine Springs Canyon, within the Mohave Desert, Mohave County, Arizona. A few of the riparian plants present are *Tamarix chinensis*, *Phragmites australis*, *Prosopis glandulosa* var. *torreyana*, *Acacia greggii*, *Equisetum* spp. and *Baccharis salicifolia*. Elevation ca. 1,220 m.

Although riparian scrublands cover many kilometers of floodplain and stream channels within the Mohavian, Chihuahuan, Madrean, and Californian provinces, there has been a tendency to ignore these biotic communities in favor of the richer biota of more structurally diverse assemblages. These communities may also constitute a riparian understory or prelude for the riparian forests just discussed, grade into marshlands or, in the more xeric places where salts accumulate, form alkali-loving communities of Saltgrass [*Distichlis spicata*] and chenopods (Gary, 1965; Bloss and Brotherson, 1979). There is ample evidence for vast increases in this formation type in past years, largely at the expense of cottonwood forests and woodland (see e.g. Turner, 1974).

Riparian scrub may range from simple disclimax consociations of introduced Saltcedar to complex and diversified associations containing dozens of species (Fig. 169). Some of the most extensive warm-temperate riparian scrublands in the Southwest are along the Río Grande from Belen, Texas, to Big Bend National Park, along portions of the Pecos River, and along the Colorado River where it traverses the Mohave desert.

Common and Giant Reeds (*Phragmites australis* and *Arundo donax*) form tall stands of "cane" along the immediate banks of the Río Grande, often extending into the stream and forming floating mats (Fig. 170). The large Goodding Willow [*S. gooddingii*] and smaller Black [*S. nigra*] and Sandbar willows (*S. interior*) also are present, along with Seepwillow [*Baccharis salicifolia*], Saltcedar, and other scrub. Other species present in riparian scrublands here (and elsewhere) include:

<i>Aster spinosus</i>	Aster
<i>Baccharis sarothroides</i>	Desert Broom
<i>Equisetum</i> spp.	horsetails
<i>Heliotropium curassavicum</i>	Heliotrope
<i>Hymenoclea</i> spp.	burrobrushes
<i>Pluchea camphorata</i>	Camphor-weed
<i>Verbesina encelioides</i>	Cowpen Daisy

Protected aquatic habitats such as cut-off ponds may support cattail, sedges, and other emergent marshland plants in addition to scrub. Pondweeds and submergent aquatic plants occur intermittently, but such communities have scarcely been described. Terraces near the Río Grande support a diverse scrubland community of Honey and Screwbean Mesquite [*Prosopis glandulosa* and *P. pubescens*], Catclaw [*Acacia greggii*], Black-brush (*A. rigidula*), Huisache [*A. farnesiana*], Desert-willow [*Chilopsis linearis*], Tree Tobacco [*Nicotiana glauca*], Common Buttonbush (*Cephalanthus occidentalis*), and Texas Paloverde (*Cercidium texanum*). Bermuda Grass (*Cynodon dactylon*) has become a major stabilizing ground cover at places where rivers scour rocky shorelines, forming extensive, lush sods (Wauer, 1973, 1977).

Canyon segments of large rivers in this climatic zone, now subjected to upstream controls, were too heavily scoured during flooding to support other than the most rudimentary riparian scrublands. This classically occurred in the Grand Canyon of the Colorado River prior to the closure of Glen Canyon Dam, wherein most riparian vegetation was a shrubby border of mesquite above the level of most annual floods (Turner and Karpiscak, 1980; Fig. 148). Similar conditions may still be found in "box" canyons of the Salt and Gila rivers in Arizona (Minckley and Clark, 1979), and of course in the central gorges of the Río Grande within Big Bend National

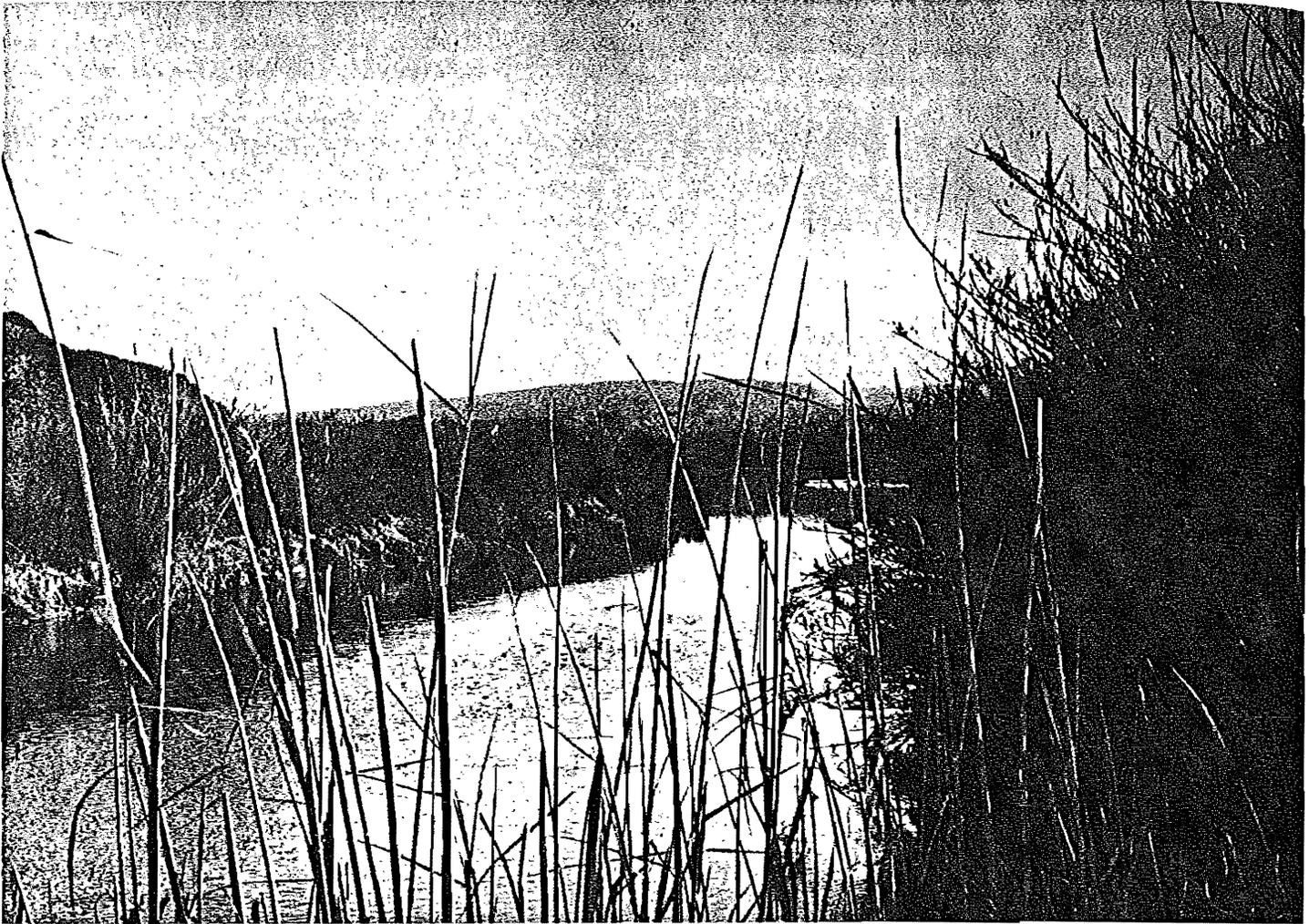


Figure 170. Riparian scrubland of reeds (*Phragmites australis*), Saltcedar (*Tamarix chinensis*), Screwbean [*Prosopis pubescens*], Buttonbush (*Cephalanthus occidentalis*) and Texas Honey Mesquite (*Prosopis glandulosa*) along the Rio Grande, in Big Bend National Park, Brewster County, Texas. Elevation ca. 750 m.

Park [Denyes, 1956]. Some of these segments have as yet resisted incursions by the aggressive Saltcedar [see Robinson 1965].

No mammals appear particularly restricted to this vegetation, although a number of bats [Easterla, 1973] as well as Cotton Rat [*Sigmodon hispidis*], White-footed Mouse (*Peromyscus leucopus*), Desert Pocket Mouse [*Perognathus penicillatus*], Beaver, and Raccoon are often well represented there [Boerr and Schmidly, 1977]. A few of the nesting birds strongly associated with riparian scrub in their appropriate biotic provinces are Crissal Thrasher (*Toxostoma dorsale*), Verdin [*Auriparus flaviceps*], Black-tailed Gnatcatcher [*Polioptila melanura*], Phainopepla [*Phainopepla nitens*], Black Phoebe [*Sayornis nigricans*], and Lucy's Warbler (*Vermivora luciae*).

The Western Spadefoot and Red-spotted Toad [*Bufo punctatus*] are, if not characteristic, two widespread and common amphibians, and Woodhouse's Toad enters the Chihuahuan Desert region only along the rivers [Conant, 1978]. In the more open scrub, the Side-blotched Lizard [*Uta stansburiana*] is perhaps the most commonly encountered reptile. Aquatic species include Spiny Softshelled Turtle [*Trionyx spiniferus*

emoryi], Pond Slider [*Chrysemys scripta*], and in the Big Bend Region, the Plain-bellied Water Snake [*Natrix erythrogaster*] [Conant, 1963, 1969, 1978].

From the mouth of the Rio Conchos downstream in the Rio Grande, and in the lowermost Pecos River, the Mississippi River fish fauna dominates. Hubbs et al. (1977) termed this the Rio Conchos-Rio Grande faunal assemblage, characterized by species such as Speckled Chub [*Hybopsis aestivalis*], Blue Sucker [*Cycleptus elongatus*], River Carpsucker [*Carpionodes carpio*], buffalofishes [*Ictiobus* spp.], Channel and Blue Catfishes [*Ictalurus punctatus* and *I. furcatus*], Red Shiner [*Notropis lutrensis*], and others. Interestingly, a tributary faunal assemblage in the same region consists of mostly species of Mexican derivation, e.g., Conchos Pupfish [*Cyprinodon eximius*], Mexican Stoneroller, Chihuahua Shiner, Mexican Tetra [*Astyanax mexicanus*], Mosquitofish [*Gambusia affinis*], Roundnose Minnow [*Dionda episcopa*], and Tamaulipas Shiner [*Notropis braytoni*], along with sunfishes [*Lepomis* spp.] and the more ubiquitous Fathead Minnow and Red Shiner.

Californian Maritime and Interior Marshlands

Marshlands of this climatic zone are represented by tidal marsh as well as a number of interior marsh biomes. In estuaries and in some protected lagoons and sheltered bays, a *Californian maritime marshland* occurs intermittently southward along the Pacific Coast to the Vizcaino Peninsula (Fig. 171). Even as far south as Scammon's Lagoon, mangroves and other tropic-subtropic species are lacking or poorly represented, and both the marshland flora and fauna have a decidedly temperate aspect.

Occurring just inland from the intertidal zone (=strand) of mud flats, sand, or (rarely) rock, these marshes are maintained and flushed by tidal action; the emergent vegetation is at or just above the high water line. As is the case with tidal marsh ecosystems almost everywhere, most of these wetlands have been greatly reduced and disturbed by human activities. Figures showing reductions in areas of marshlands in Mission Bay, San Diego Bay, and Tijuana Estuary are especially impressive (MacDonald, 1977). Much of these and other coastal marshlands once found in southern California have been destroyed; small marshes, such as the one at Newport Bay, have been preserved only after considerable effort. The best examples of warm temperate maritime marshland remaining in the Southwest are in Baja California del Norte, the most extensive in the vicinity of Scammon's Lagoon.

Emergent vegetation in these marshes is most often consociations of either cordgrass (*Spartina foliosa*), or at slightly higher sites subject to less inundation, Pickleweed (*Allenrolfea occidentalis*), or Glasswort (*Salicornia virginica*). This latter species colors an otherwise sedate marsh, turning reddish orange in autumn and harboring the bright orange parasitic Dodder [*Cuscuta salina*] in spring and summer. Other beach and marsh plants as Batis [*Batis maritima*], Saltgrass [*Distichlis spicata*], Marsh-rosemary or Sea-lavender [*Limonium californicum*], Seep-weed [*Suaeda californica*], *Monanthochloë littoralis*, Arrowgrass [*Triglochin maritima*], *Salicornia subterminalis*, *Jaumea carnosa*, and *Anemopsis californica*, while widespread, are only rarely dominant. Although communities of Giant Bulrush (*Scirpus californicus*), rushes, and even cattail may be present in the brackish waters of some estuaries, such situations are uncommon in the Southwest. Saltbushes (*Atriplex patula* and others) and Alkali-heath (*Frankenia grandifolia*) may occupy mounds and other relatively xeric locales within the marsh. The only annual of consequence is *Salicornia bigelovii* (Macdonald, 1977).

Few birds nest in Californian maritime marshlands, the endangered Light-footed Clapper Rail (*Rallus longirostris levipes*) and Black Rail (*Laterallus jamaicensis*) being two important exceptions. Nonetheless, a great variety of migrating and wintering shore and marsh birds make these wetlands particularly attractive to bird watchers. Species especially found here or in adjacent strands include:

<i>Calidris melanotos</i>	Pectoral Sandpiper
<i>C. minutilla</i>	Least Sandpiper
<i>Catoptrophorus semipalmatus</i>	Willet
<i>Himantopus mexicanus</i>	Black-necked Stilt
<i>Limnodromus griseus</i>	Short-billed Dowitcher
<i>L. scolopaceus</i>	Long-billed Dowitcher
<i>Limosa fedoa</i>	Marbled Godwit
<i>Numenius americanus</i>	Long-billed Curlew
<i>N. phaeopus</i>	Whimbrel
<i>Nycticorax nycticorax</i>	Black-crowned Night Heron

<i>Recurvirostra americana</i>	American Avocet
<i>Totanus flavipes</i>	Lesser Yellowlegs
<i>T. melanoleucus</i>	Greater Yellowlegs
<i>Tringa solitaria</i>	Solitary Sandpiper

The larger marshes are (or were) also used by numerous wintering waterfowl, as for nighttime resting and feeding by wintering Black Brant (*Branta nigricans*).

Amphibians are understandably absent from saline maritime marshes, and reptiles are scarcely represented in brackish waters by Western Pond Turtle (*Clemmys matmorata*) and two garter snakes (*Thamnophis sirtalis* and *T. elegans*), near inflowing streams. Fishes are variously represented depending on salinity, water depth, and permanency. Marine species that characteristically move into brackish Californian marshes include Shiner Perch (*Cymatogaster aggregata*), Arrow and Tidewater Gobies (*Clevelandia ios* and *Eucyclogobius newberryi*), Longjaw Mudsucker (*Gillichthys mirabilis*), and Starry Flounder (*Platichthys stellatus*). Three-spine Stickleback and California Killifish also are characteristic of marshy areas along southern California coastlines, and the killifish successfully occupies hypersaline waters to 128 g/l (Miller and Lea, 1972).

Inland, other warm-temperate marshlands occur in old river oxbows, on poorly drained lands, at springs and other shallow water sites in the Californian, Mohavian, Madrean, and Chihuahuan biotic provinces (Figs. 172, 176). Many of these represent remnants of once large aquatic systems, the great Pluvial lakes and rivers of the west (Hubbs and Miller, 1948; Reeves, 1969; Strain, 1970; Hubbs et al., 1974), now scarcely perpetuated by far lower precipitation and meager outflows of groundwater. Many of these environments are saline, a result of evaporative concentration of salts in endorheic basins, and plant communities often are reminiscent of seaside marshes.

Remnant springs and marshes of pluvial Lake Manly in Death Valley are generally surrounded by saltgrass (Fig. 173) and scattered clumps of Common Reed. Small rushes (*Juncus cooperi*, *Nitrophila occidentalis*) are associated with saltgrass in wetter areas. The edges of open water are occupied by bulrushes, principally *Scirpus americanus* and with lesser frequency *S. maritimus* var. *macrostachyus*. Lizardtail (*Anemopsis californica*) is a characteristic species near seeps (Bradley, 1970). In other parts of the Death Valley system, as in Ash Meadows where salts are less concentrated, marshes in spring outflows are backed by extensive scrublands of mesquite and other woody plants (Beatley, 1971). These areas now are suffering invasion by Saltcedar in a pattern similar to that described for riparian wetlands.

Inland marshes are most extensive in the Chihuahuan biotic province, in the remarkable number of bolsones of that region (Figs. 174, 175, 176). These Chihuahuan interior marshlands are subject to great variation in the length and frequency of inundation, and some may be dry for periods of a year or more (Henrickson, 1978), with broad strands surrounding zones of permanent water.

Deeper and better watered locales and springs [e.g., the Cuatro Ciénegas Basin in Coahuila, Mexico], where salinities are not too high, support complex communities of cattail (*Typha angustifolia*), bulrushes, and Common Reed. Lesser sedges and grasses [*Eleocharis cellulosa*, *E. rostellata*, *E. caribaea*, *Carex pringlei*, *Spartina spartinae*, and *Setaria geniculata*] may develop as an understory or as monospecific stands. Drier

shorelines are covered by grasses and sedge including *Fimbristylis thermalis*, *Fuirena simplex*, and *Schoenus nigricans* [see e.g., Fig. 175].

Herbaceous plants of this assemblage include Heliotrope, Water Hyssop [*Bacopa monnieri*], Water Primrose [*Ludwigia octovalvis*], Lizard Tail, Water Parsnip [*Berula erecta*], and many others. In open water, Waterlily [*Nymphaea ampla*], Bladderwort (*Utricularia obtusa*), and charophytes often are common, as are species of pondweed (*Potamogeton nodosus*, *P. pectinatus*), Holly-leaf Naiad (*Najas marina*), Widgeon-grass [*Ruppia maritima*], and Common Pondmat [*Zannichellia palustris*] (Pinkava, 1978).

The few and, therefore, particularly valuable cattail and other marshlands within the Western warm-temperate provinces provide "oases" to widely separated populations of nesting and migrating marsh birds. Even the smallest of these seem to support a family of Red-winged Blackbirds, Coots, and Long-billed Marsh Wrens (*Cistothorus palustris*). Both the larger natural wetlands, such as those in Chihuahua [lagunas Baviçora, Santa María, Mexicanos, and Patos] and "managed" marshes such as at Bosque del Apache National Wildlife Refuge, Willcox Playa, Lake McMillan, and San Simón Ciénega in New Mexico and Arizona, may provide nesting habitat for the endemic Mexican Duck (*Anas platyrhynchos diazi*) (O'Brien, 1975). Other waterfowl, such as Snow Geese [*Chen caerulescens*], Pintails [*Anas acuta*], Green-winged Teal [*A. crecca*], American Widgeon (*Anas americana*), and Shovelers [*Spatula clypeata*], use these marshes during migration, and there is some nesting by Blue-winged Teal (*Anas discors*), Cinnamon Teal (*Anas cyanoptera*), Ruddy Ducks (*Oxyura jamaicensis*), and Avocets and other marsh birds. During winter months these marshlands and adjacent playa strands may provide roosting sites for large concentrations of Sandhill Cranes.

Marshlands sometimes support dense populations of aquatic amphibians, especially after heavy runoff expands available water and/or dilutes saline conditions. Included there are many desert and grassland species, spadefoot toads [*Scaphiopus* spp.], true toads [*Bufo cognatus*, *B. debilis*], and Tiger Salamander, which are preyed upon by the ever-present garter snakes.

Few mammals are restricted to these interior marshlands, but springfed pools and seeps should be as important to bats moving over arid lands as they are to migrating birds (O'Farrell and Bradley, 1970). In Death Valley, it has been demonstrated that the moister areas near marshes enhance populations of desert rodents, including Round-tailed Ground Squirrel (*Spermophilus tereticaudus*), Desert Kangaroo Rat (*Dipodomys deserti*), Harvest Mouse [*Reithrodontomys megalotis*], and Desert Woodrat [*Neotoma lepida*] (Bradley and Deacon, 1971; Sulley et al., 1972). Mesic marshlands also may allow northern or high-altitude mammalian species to persist in lowlands, e.g., Vagrant Shrew [*Sorex vagrans*] on isolated mountains in southern Arizona (Cockrum, 1960) and Meadow Vole [*Microtus pennsylvanicus*] in springfed marshes near Galeana, Chihuahua (Cockrum and Bradley, 1968).

Warm temperate wetlands support an inordinate number of fishes in the Southwest. This largely results from extreme isolation and substantial security, afforded by desert springs, and the presence of a remarkable family of fishes, the Cyprinodontidae, which has members adapted for survival in some of the most severe aquatic habitats yet described. Well-

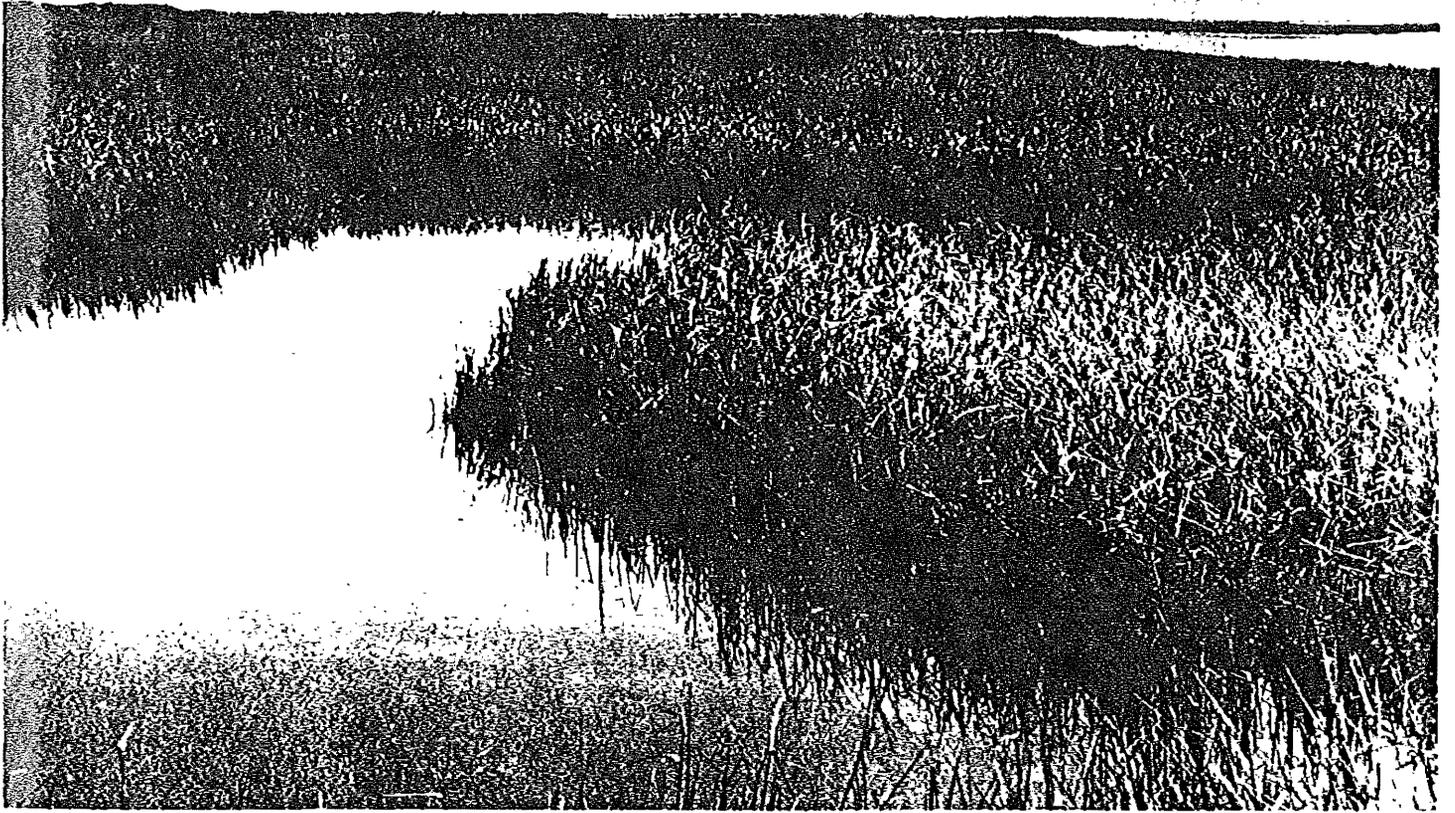


Figure 171. Californian maritime marshland at Laguna Manuela, Baja California del Norte, Mexico. Emergent vegetation is a consociation of Cordgrass [*Spartina foliosa*].



Figure 172. Interior (Sonoran) marshland, woodland, and submergents at Arivaca Slough, Pima County, Arizona (winter aspect). Although there is often much integration, there also is often only one or two representative dominants in each formation-class—in this case cattail [*Typha domingensis*] marshland and willow [*Salix gooddingii*] woodland. Elevation ca. 1,100 m.



Figure 173. Interior (Mohavian) marshland along Salt Creek, Death Valley National Monument, San Bernardino County, California. Consociations of Salt Grass (*Distichlis stricta*; drier areas) and Bulrush (*Scirpus olneyi* in the water), with few associates, line this marsh-stream. Elevation ca. -25 m; photograph by Stuart G. Fisher, November 1979.

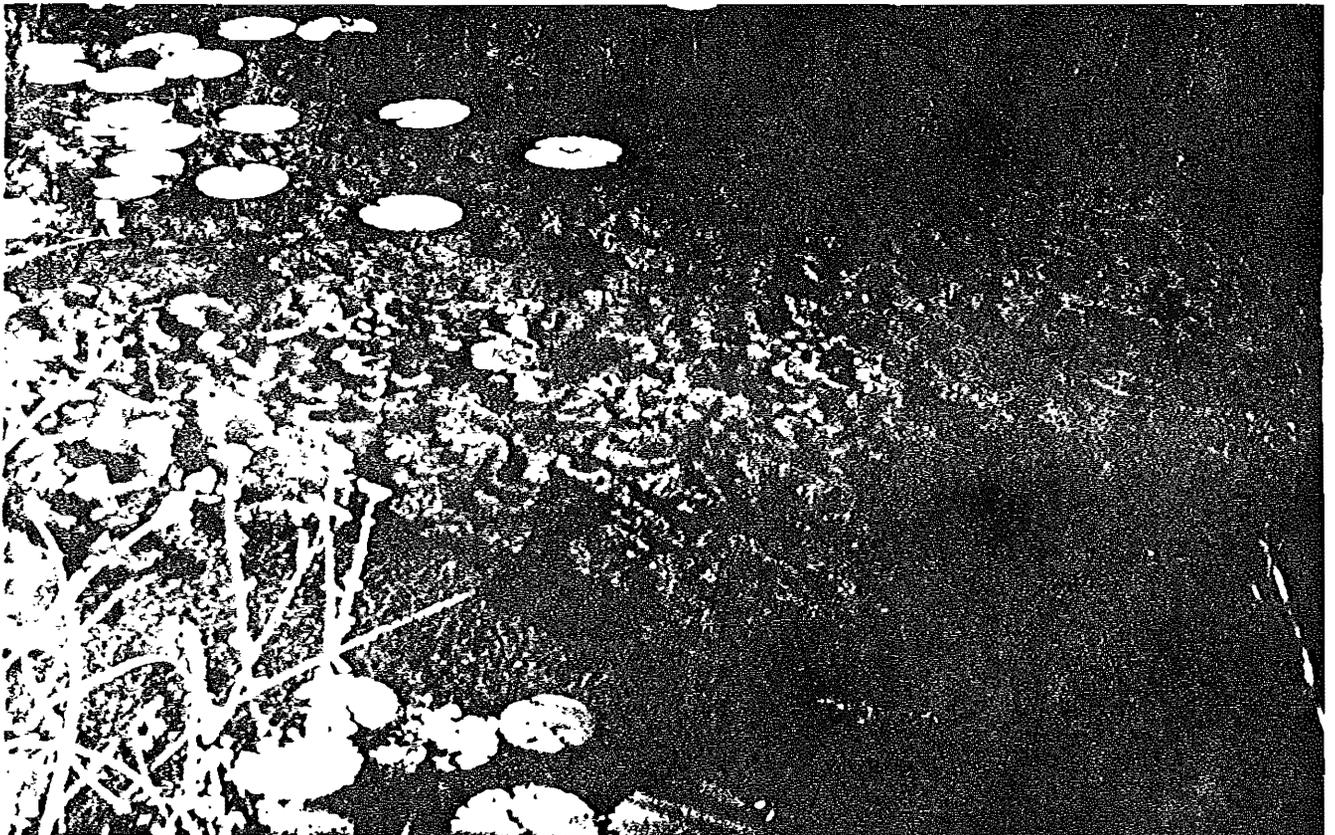


Figure 174. Sub- and emergent growth-forms of *Nymphaea ampla* in clear, 1.5-m-deep water of Laguna Tio Candido, Cuatro Ciénegas Basin, Coahuila, Mexico; Elevation ca. 750 m; photograph by W.L. Minckley, December 1979.

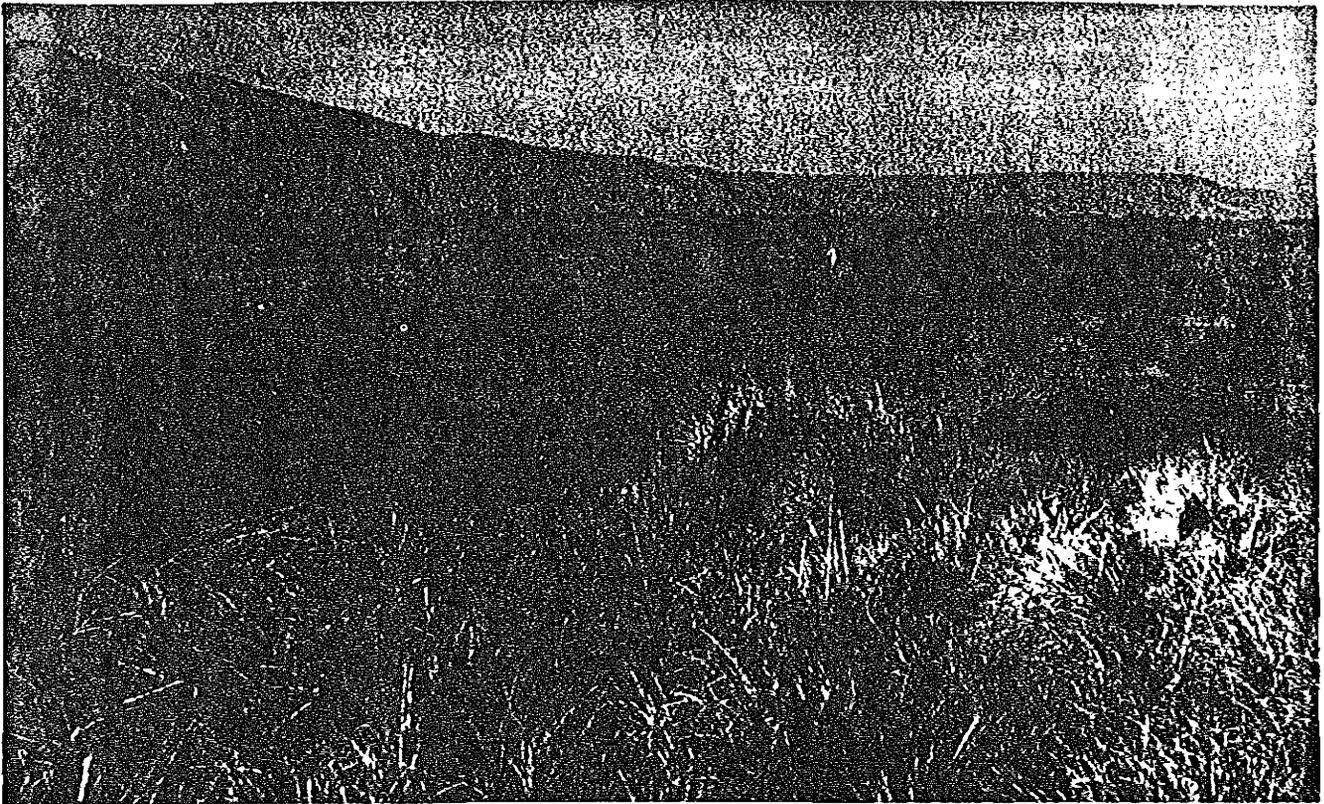


Figure 175. *Laguna Tio Candido and associated marshes. A complex submergent and marshland community, including *Typha angustifolia*, *Scirpus olneyi*, and lesser aquatics, with drier shorelines vegetated by *Fimbristylis thermalis*, *Fuirena simplex*, *Schoenus nigricans*, and *Sporobolus* sp. Elevation ca. 750 m; photograph by W.L. Minckley, December 1979.*

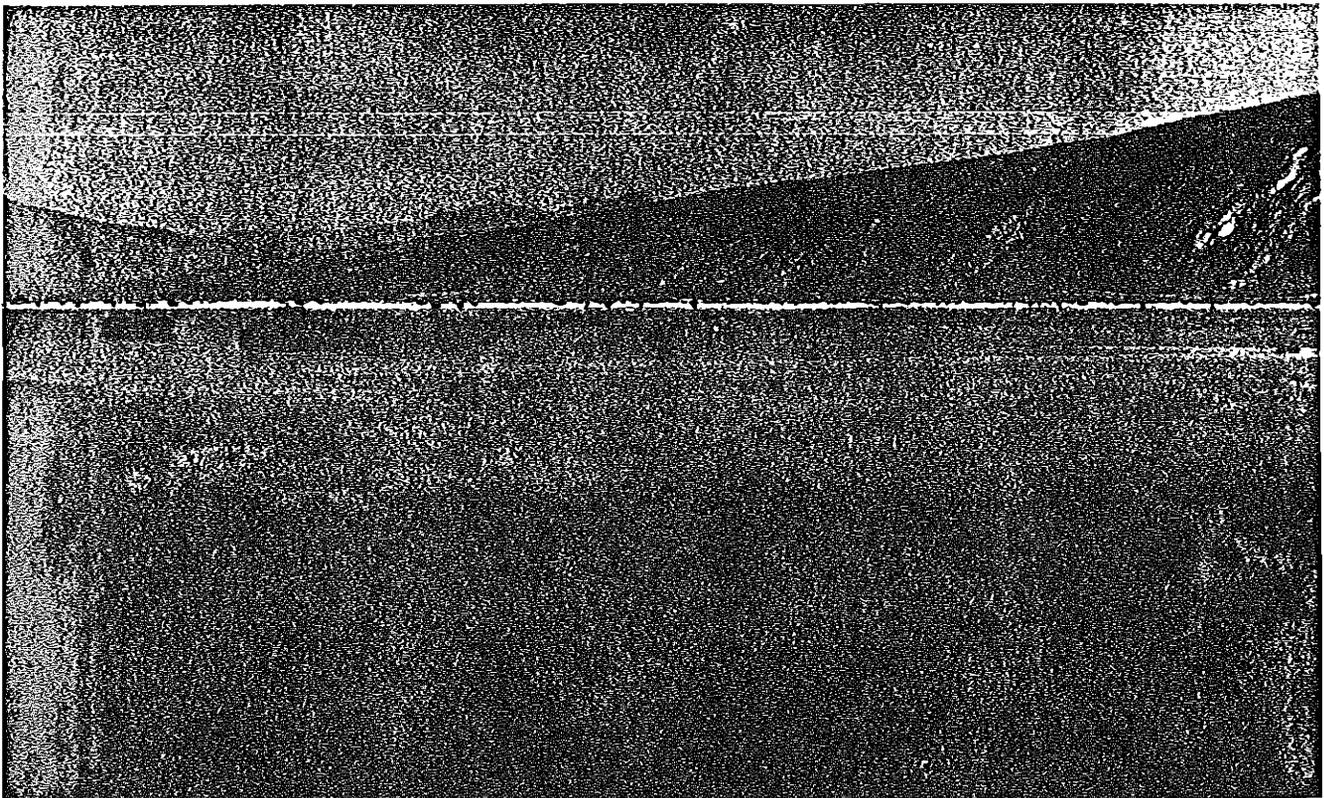


Figure 176. *Interior (Chihuahuan) marshland near the inflow of Rio Churince to Laguna Grande, Cuatro Ciénegas Basin, Coahuila, Mexico; flooded Salt Grass [*Distichlis stricta*] dominates the saline flats surrounding this barrier lake, with clumps of sedges [*Scirpus olneyi* and others] occurring in less severe areas near the inflowing stream; dunes in background result from wind transport from the lake margin during drier periods (see also Fig. 179). Elevation ca. 750 m.*

watered Pluvial environments allowed for dispersal of these fishes, along with a few other groups (coarse-scaled species of *Gila*, some *Catostomus*, and Speckled Dace), and when those rivers and lakes dried, the fishes remained to exploit meager remnants. If the riverine Pecos, Conchos, and Red River pupfishes are excluded, the other pupfish species listed in Table 32 from the Rio Grande-Pecos River systems are presently restricted to springs and spring-fed habitats, as are most of the mosquitofishes (excluding *Gambusia affinis* and *G. senilis*). Thus each of these genera is today prepared for natural desiccation with representatives positioned to survive all but human-caused catastrophe, such as pumpage resulting in lowering of water tables.

In the Death Valley system, the Mojave River has a single endemic—the Mohave Chub (*Gila bicolor mohavensis*). The higher-elevation Owens River has four: the Owens Tui Chub (*G. bicolor snyderi*), Owens Sucker (*Catostomus fumeiventris*), Owens Pupfish (*Cyprinodon radiosus*), and a distinctive Speckled Dace (Miller, 1973). The Amargosa River basin, including Death Valley itself and Ash Meadows, had a distinctive Speckled Dace and seven species of pup- and poolfishes: Amargosa Pupfish (*Cyprinodon nevadensis*), Salt Creek Pupfish (*C. salinus*), Cottonball Marsh Pupfish (*C. milleri*), Devil's Hole Pupfish (*C. diabolis*), Pahrump Poolfish (*Empetrichthys latos*), and the recently extirpated Ash Meadows Poolfish (*E. merriami*). These are separated into no fewer than 14 subspecies (Miller, 1948; Soltz and Naiman, 1978).

The remarkable Cuatro Ciénegas Basin in Coahuila, Mexico, is the only other desert bolsón to demonstrate a similar degree of endemism as Death Valley. Comparison of Tables 32 and 33 reveals the distinctiveness of the Cuatro Ciénegas fish fauna, which includes 15 of a total of 20 species that are known only from, or are differentiated within, that small area (Minckley, 1969, 1978). Endemism in invertebrates (Taylor, 1966; Minckley, 1978), other vertebrates as the aquatic Coahuilan Box Turtle (*Terrapene coahuiliana*) (Brown, 1974), other endemic turtles (*Trionyx ater*, *Chrysemys scripta taylori*) (Conant, 1978), terrestrial forms such as *Gerrhonotus lugoi* (McCoy, 1970), and numerous vascular plants (Pinkava, 1978), plus a remarkable assemblage of relict species (Milstead, 1960), further attest to the antiquity of aquatic and terrestrial habitats of that area (Meyer, 1973). Most other basins of the Chihuahuan Desert have lesser, but nonetheless significant, levels of endemism: the basin of Lago de Guzmán in northern Chihuahua and southern New Mexico contains at least three pupfishes and the endemic Chihuahua Chub (*Gila nigrescens*), and Laguna de Bavicora supports a species of *Gila*.

Some species of fishes in desert springs are stenotherms, adapted to narrow temperature ranges of their special environments. The most spectacular of these is perhaps the Moapa Dace (*Moapa coriacea*) and some populations of springfish (*Crenichthys baileyi*, *C. nevadae*) of the Pluvial White River of Nevada. These animals live within a few degrees of what is considered lethal maxima for many fishes, between 30.5° and 34° C for the dace and up to 35° for *C. baileyi*, and at least *M. coriacea* does not venture into cooler waters (Deacon and

Bradley, 1972). Indeed, certain populations of these animals are protected from depredations and competition from introduced fishes by high temperatures that only they can withstand; most introduced species simply cannot invade the thermal environments enjoyed by these natives.

Development of water resources adjacent to marshlands in the interior Southwest spells doom for many of the special habitats just discussed. Lowering of water tables obviously destroys surface waters of a permanent nature, and obligate aquatic communities disappear. If waters persist, non-native organisms provide other problems. Severity of this situation was recently pointed out by Pister (1974) as follows (brackets ours):

"During the past 35 years, man's activities apparently have caused the extinction of 4 species and 6 subspecies in 6 genera [of fishes] within California, Nevada and Arizona. In addition, at least 50 species and subspecies in 26 genera within 8 Great Basin States and northern Mexico are considered threatened. 19 of which are currently listed as endangered by the Secretary of the Interior... This situation has resulted primarily from agricultural pumping and diversion of watercourses and has been aggravated by the introduction of predaceous game fishes and other piscine competitors."

At this writing his statement stands true, and additional taxa may soon be added to Pister's ominous statistics.

Table 33. Fishes of the Cuatro Ciénegas basin, Coahuila, Mexico. Symbols: * = restricted to the basin; ** = differentiated to the subspecific level within the basin when compared to materials from the lower Rio Grande into which Cuatro Ciénegas water now flows as a result of canal connection via Rio Salado [from Minckley, 1978].

Characidae	Poeciliidae (cont'd)
<i>Astyanax mexicanus</i> (Mexican Tetra)	* <i>Xiphophorus gordonii</i> (Cuatro Ciénegas Platyfish)
Cyprinidae	Centrarchidae
* <i>Notropis xanthicara</i> (Cuatro Ciénegas Shiner)	** <i>Lepomis megalotis</i> (Longear Sunfish)
** <i>Dionda episcopa</i> (Roundnose Minnow)	** <i>Micropterus salmoides</i> (Largemouth Bass)
Ictaluridae	Percidae
** <i>Ictalurus lupus</i> (Headwater Channel Catfish)	* <i>Etheostoma</i> sp. (Cuatro Ciénegas Darter)
<i>Pylodictis olivaris</i> (Flathead Catfish)	Cichlidae
Cyprinodontidae	<i>Cichlasoma (Herichthys) cyanoguttatum</i> (Rio Grande Perch)
* <i>Lucania interioris</i> (Interior Killifish)	<i>Cichlasoma (Herichthys) sp.</i>
* <i>Cyprinodon bifasciatus</i> (Laguna Pupfish)	* <i>Cichlasoma (Parapetenia) sp.</i> "A" ("Lugo's Cichlid")
* <i>Cyprinodon atrorus</i> (Ciénega Pupfish)	* <i>Cichlasoma (Parapetenia) sp.</i> "B" ("Caracole Cichlid")
Poeciliidae	* <i>Cichlasoma (Parapetenia) sp.</i> "C" ("Longhead Cichlid")
* <i>Gambusia longispinis</i> (Cuatro Ciénegas Mosquitofish)	* <i>Cichlasoma (Parapetenia) sp.</i> "D" ("Unexpected Cichlid")
<i>Gambusia marshi</i> (Rio Salado Mosquitofish)	

Californian Maritime Strands

Although strand vegetation occupies numerous, if not extensive, interior habitats, this formation is most often considered in context of those beach communities occurring between low tide and the influence of the highest tide (=intertidal zone). There the barrenness of vegetation caused by wave action, saline water tables, shifting sandy substrates, salt spray, and sand blast, corresponds to the desertscrub formation of upland vegetation. As in interior habitats, substrates may be rock, sand, or mud. In the warm temperate Southwest, coastal vegetation is represented by *Californian maritime strand*, which has been well described by Barbour and Johnson [1977].

The Californian coastline is characterized by rocky cliff and tidepool environments, sandy beaches and dunes, and more rarely, salt marsh and mud flats (Fig. 177). Dunes and sandy beaches are confined to bays [e.g., Long Beach]. Beaches tend to build seaward in summer and erode during winter months, and the spring tidal range is moderate (Hinton, 1969).

Strand vegetation in California varies greatly from north to south—forbs dominate south of 34°N and the plants are mostly prostrate, herbaceous, evergreen, and succulent. Vegetation increases landward toward the foredunes; dune vegetation commonly grades into coastal scrub and may be composed of open communities of the same species. The species as well as density of vegetation also follows a zonation based on environmental tolerances. In the Southwest, the number of species in the littoral strip is few, some of the most common and characteristic being the Saltbush (*Atriplex leucophylla*), Sand-verbena (*Abronia maritima*), Silver Beachweed (*Ambrosia chamissonis*), Evening-primrose [*Oenothera cheiranthifolia*], Goldenweed (*Haplopappus venetus*), Mock Heather (*Haplopappus ericoides*), *Lupinus chamissonis*, *Abronia umbellata*, and the Ice Plant (*Mesembryanthemum crystallinum*). Introduced species such as *Mesembryanthemum chilense*, *Monanthochloë littoralis*, and the Beach Morning Glory (*Calystegia soldanaella*) are now important in the strand makeup, and the annual *Cakile maritima* is commonly the last vascular plant to seaward before submergents are encountered. On dunes north of San Diego one may find the introduced Beachgrass (*Ammophila arenaria*).

Although the number and variety of sandpipers, gulls, stilts, plovers, and other shorebirds during migration and in winter is especially large in this habitat, the numbers of nesting species that use such places in the Southwest is not. Furthermore, many of these are now, because of human disturbance, confined to islands and the few available remote sites. In the Southwest, some of the most common or indicative species are:

<i>Charadrius alexandrinus</i>	Snowy Plover
<i>Endomychura hypoleuca</i>	Xantus' Murrelet
<i>Huematopus bachmani</i>	Black Oystercatcher
<i>Larus occidentalis</i>	Western Gull
<i>Phalacrocorax auritus</i>	Double-crested Cormorant
<i>P. penicillatus</i>	Brant's Cormorant
<i>Sterna albitrons</i>	Least Tern
<i>Thalasseus elegans</i>	Elegant Tern

Some of the rockier headlands and offshore habitats support rookeries of California Sea Lion (*Zalophus californianus*), and sand bars, reefs, and spits are calving sites for the Harbor Seal (*Phoca vitulina*). Two former breeding pinnipeds of the mainland strand of southern California and

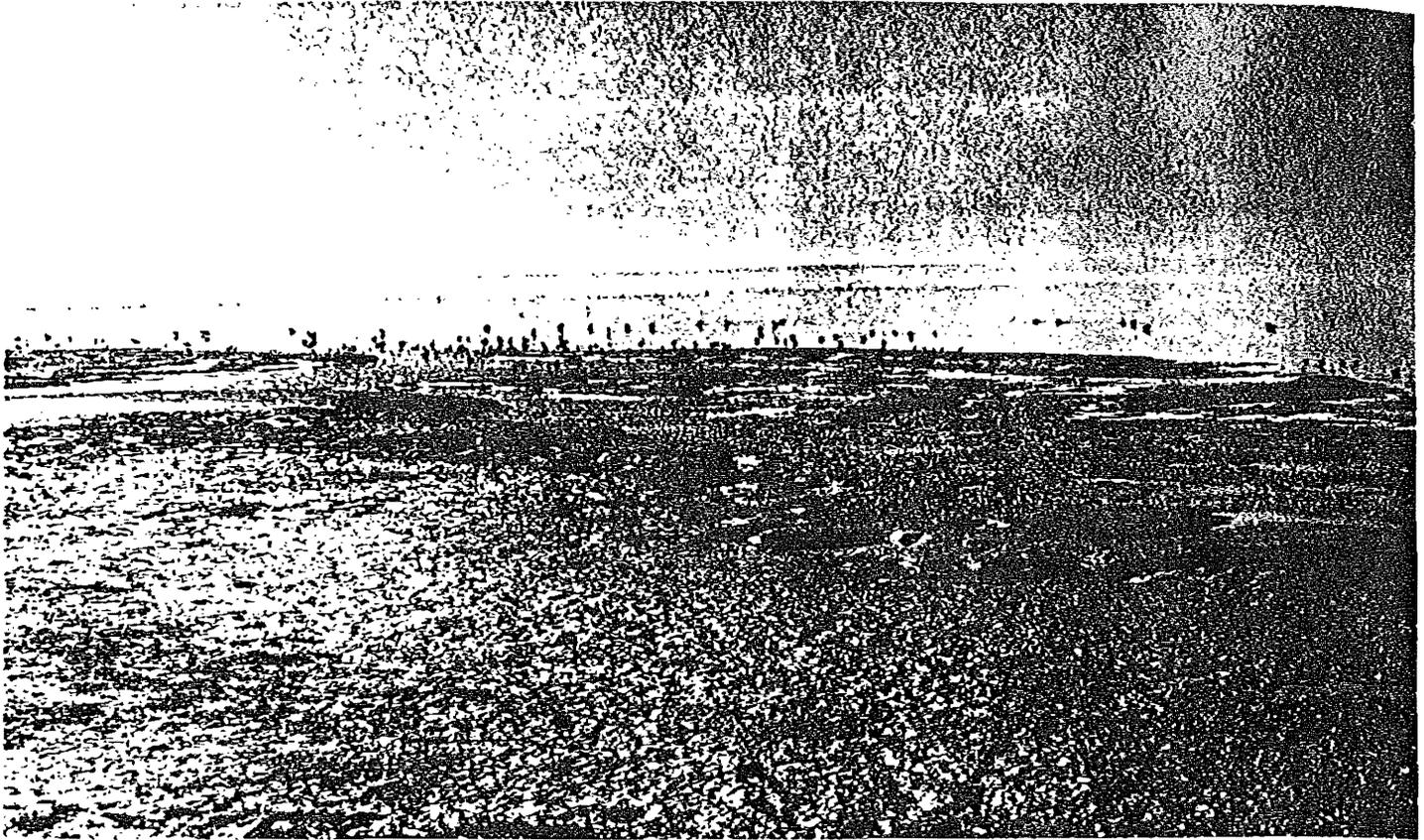


Figure 177. Californian maritime strand at Scammon's Lagoon, Baja California del Norte, Mexico. These "mud flats" at low tide at first appear unvegetated, but closer inspection reveals prostrate seagrasses, diverse algae, and other plant life in addition to a rich, depression- and burrow-inhabiting invertebrate and vertebrate fauna.

northern Baja California, the Elephant Seal (*Mirounga angustirostris*) and Guadalupe Fur Seal (*Arctocephalus townsendi*), are making a comeback and are now in the process of reoccupying many of their former breeding islands (Hubbs et al., 1965, 1968). These large animals, plus other mammals and fishes, provided carrion in strand areas which served as food for special raptors such as California Condor (*Gymnogyps californianus*).

Rocky bays, shorelines, and tidepools of the California coast support a diversity of fishes (Miller and Lea, 1972; Fitch and Lavenberg, 1975). Bay, Rockpool, and Mussel Blennies [*Hypsoblennius gentilis*, *H. gilberti*, *H. jenkinsi*] are common, as are clinid blennies [*Gibbonsia* spp.], and cottids or sculpins [*Clinocottus analis*, *Oligocottus rubellio*], Zebra and Bluebanded Gobies [*Lythrypnus zebra*, *L. dalli*], Yellowfin Goby [*Acanthogobius flavemanos*], and the unique Blind Goby [*Typhlogobius californiensis*] that lives in close-spaced habitats beneath rocks. Clingfish [*Gobiesox meandricus*] occur on wave-washed rocks and can withstand several hours out of water if in a moist place. The Rockweed Gunnel (*Xerperes fucorum*) was said by Barnhart (1936) to move freely over stones or sand out of water at low tides.

Shore fishes that move into strand areas at high tide include Needlefish (*Strongylura exilis*), Jack Smelt (*Atherinopsis californiensis*), White Seabass and Orangemouth Corvina [*Cynoscion nobilis*, *C. xanthurus*] and Yellowfin Croaker (*Umbrina roncadori*). Other species are more common in bays,

e.g., Cabezón (*Scorpaenichthys marmoratus*), Silver Mojarra (*Euclinostomus argenteus*), or have young that inhabit rock-pools and adults that move to deeper, inshore areas: Gopher Rockfish [*Sebastes auriculatus*], Black-and-Yellow Rockfish [*S. chrysomelas*], and Opaleye (*Girella nigricans*). The unique surfperches (Embiotocidae) of the California coast live in shallow bays and along sandy shorelines. This live-bearing group includes numerous species (Tarp, 1952), among which the Shiner and Silver Surfperches (*Cymatogaster aggregata*, *Hyperprosopon ellipticum*) are perhaps most familiar, one species of this large group is freshwater (Tule Perch, *Hystero-carpus traskii*) in the Sacramento-San Joaquin system north of our area. Perhaps the most indicative strand fish of southern California is the Grunion (*Leuresthes tenuis*), which reproduces at high tide in spring and summer. The female buries in the sand, tail down to its pectoral fins. Eggs are spawned and fertilized by sperm that moves through the sand. The eggs remain for 2 weeks longer, until dislodged by the next series of high tides, and embryos break free upon contact with water. Other, related species such as Jack Smelt spawn on eelgrass within the zone of the lowest tides.

Soft bottoms in bays are inhabited by similar shoreline fishes at high tide, and by cryptic forms as Worm-hole or Shadow Goby (*Quietula y-cauda*) that inhabits burrows of invertebrates, or Arrow Goby (*Clevelandia ios*) and Longjaw Mudsucker (*Gillichthys mirabilis*) that persist at low tide in shallow depressions or holes in wet mud.

Warm-Temperate Interior Strands

Strand habitats also occur in flood channels of rivers, along banks of streams below hydroelectric dams, along receding reservoirs, and around intermittent fluctuating lakes. Vegetation of these harsh environments is made up of either short-lived successional species or plants adapted to periodic flooding, scouring or soil deposition, and in the case of playa lakes, high salinities or other special chemical conditions associated with evaporation of inland waters. Depending on substrate and frequency and type of inundation, interior strand communities along streams may be composed of sparse, open stands of riparian scrub species (e.g., *Baccharis salicifolia* and *Tamarix chinensis*), seedlings of riparian trees such as willows and cottonwood, or any of a number of characteristic annuals, biennials, and short-lived perennials, or barren except for simple plants such as algae (Fig. 178).

A narrow strand occurs along the mainstream Colorado River, within Grand Canyon, downstream from Glen Canyon Dam, where stability is provided by upstream dams that produce an almost-tidal, daily fluctuation in water levels. Sandbars and other available substrates are vegetated sparsely by Saltcedar, Coyote Willow, Seepwillow, and the introduced Camelthorn. This zone is an example of a remarkable exchange of materials from aquatic to terrestrial systems, with great numbers of aquatic invertebrates, principally the Scud [*Gammarus lacustris*] stranded in drifting algae, feeding ants and other streamside invertebrates as well as a myriad of vertebrates ranging from iguanid lizards [e.g., *Sceloporus magister*, *Urosaurus ornatus*], to insectivorous birds and raccoons.

Upstream from dams, along the margins (strands) of fluctuating reservoirs, Bermuda Grass may occupy a large percentage of the soil surface, growing rapidly downslope as waters are removed for irrigation or power production. It provides meadows heavily used by cottontail, jackrabbits and, in season, flocks of geese and ducks. Flooding of these grassy areas adds substantial nutrients to aquatic systems when high waters occur after snowmelt or summer monsoons. When southwestern reservoirs are relatively stabilized, with daily and annual fluctuations of less than a few meters, clumps of Common Reed [*Phragmites australis*] establish, floating on the water surface on the lakeward side during high water and settling to root at the water's edge when lake levels are down.

A number of shore and other coastal strand birds are equally adapted to interior strands along rivers and reservoirs. These include Spotted Sandpiper (*Actitis macularis*)—rocky stream channels during migration and in winter (grasses and marshlands used for nesting); Killdeer (*Charadrius vociferus*)—open ground, gravel bars; Rough-winged Swallow (*Stelgidopteryx ruficollis*)—cutbanks of streams; and Black Phoebe (*Sayornis nigricans*)—overhanging walls of canyon-bound creeks and rivers. Isolated sand bars are heavily used by wintering Canada Geese (*Branta canadensis*) and other waterfowl as a nighttime resting place and as a source of gravel. Raccoons are otherwise perhaps the most frequent homeotherms occupying inland strands while foraging at night, and a number of other scavengers, as along seacoasts, depend upon this zone for carrion, e.g., the Bald Eagle (*Haliaeetus leucocephalus*) and lesser, stream-dependent raptors such as the Black Hawk.

Inland river strands are also depended upon by the Spiny Softshell Turtle for basking and oviposition, and are similarly



Figure 178. Riparian strand along the San Pedro River within the Chihuahuan Desert south of Cascabel, Cochise County, Arizona. A seasonally inundated mud-sand substratum populated by a few plants of Burrobrush (*Hymenoclea monogyra*) and nightshade [*Solanum* spp.]. Elevation ca. 1,000 m.

used by other aquatic turtles in areas where they occur. Garter snakes, toads (*Bufo woodhousei*, *B. microscaphus*), and other, less aquatic adapted species, forage in strand. Debris and other sparse cover along streams and lakes may be occupied by frogs, principally the Leopard Frog; they are rarely found on open beaches or gravel bars where they would be highly vulnerable to aerial predators. No fishes regularly use the strand zone. However, the substantial nutrients derived from periodically flooded vegetation and debris undoubtedly enhance fishes and other aquatic organisms. Flood-deposited debris is processed by terrestrial reducers in this zone when dry, converting it to smaller particles that can more easily be used by the aquatic system (Bruns and Minckley, 1980).

Within the fluctuation zones of interior playa lakes even greater selection pressures come to bear. Salts accumulated in the vast internal drainage basins of the Southwest, especially in the Chihuahuan Desert where well over 300,000 km² are endorheic, often are sufficiently concentrated to affect water uptake by plants. Because these saline accumulations are periodically inundated, they qualify as strand, and many of the plants occurring there are the same as in maritime

situations. Vegetation, if present, consists of one or a few pioneer species including *Allenrolfea occidentalis*, Salt Grass, Sea-purslane (*Sesuvium verrucosum*), species of *Suaeda* [*S. jacoensis*, *S. palmeri*, *S. fructicosum*], *Salicornia rubra*, and the halophytic Lovegrass [*Eragrostis obtusiflora*]. A single species at low density often comprises the sole vegetation of such areas. Common species on higher, less frequently flooded and less saline habitats include *Atriplex acanthocarpa*, *A. obovata*, and other saltbushes, sacatón grasses (*Sporobolus arioides*, *S. wrightii*) and *Suaeda* spp. Even the most salt tolerant plants often grow at low to non-saline conditions, thus the "pioneers" listed above also live in other communities. *Allenrolfea occidentalis*, although characteristic of playa habitats (Ungar, 1974), is among the desertscrub on bajada slopes where individual plants may reach 2 m in height (Pinkava, 1978). However, severe saline strand habitats appear to have selected for an unique inland flora. Of 40 taxa considered halophytic in the Chihuahuan Desert, 25 (including 3 genera) are endemic to such areas (Henrickson, 1978).

Many species germinate and develop on these saline sites only after rains temporarily decrease soil salts, then die as salinity again increases. Annual grasses in this category

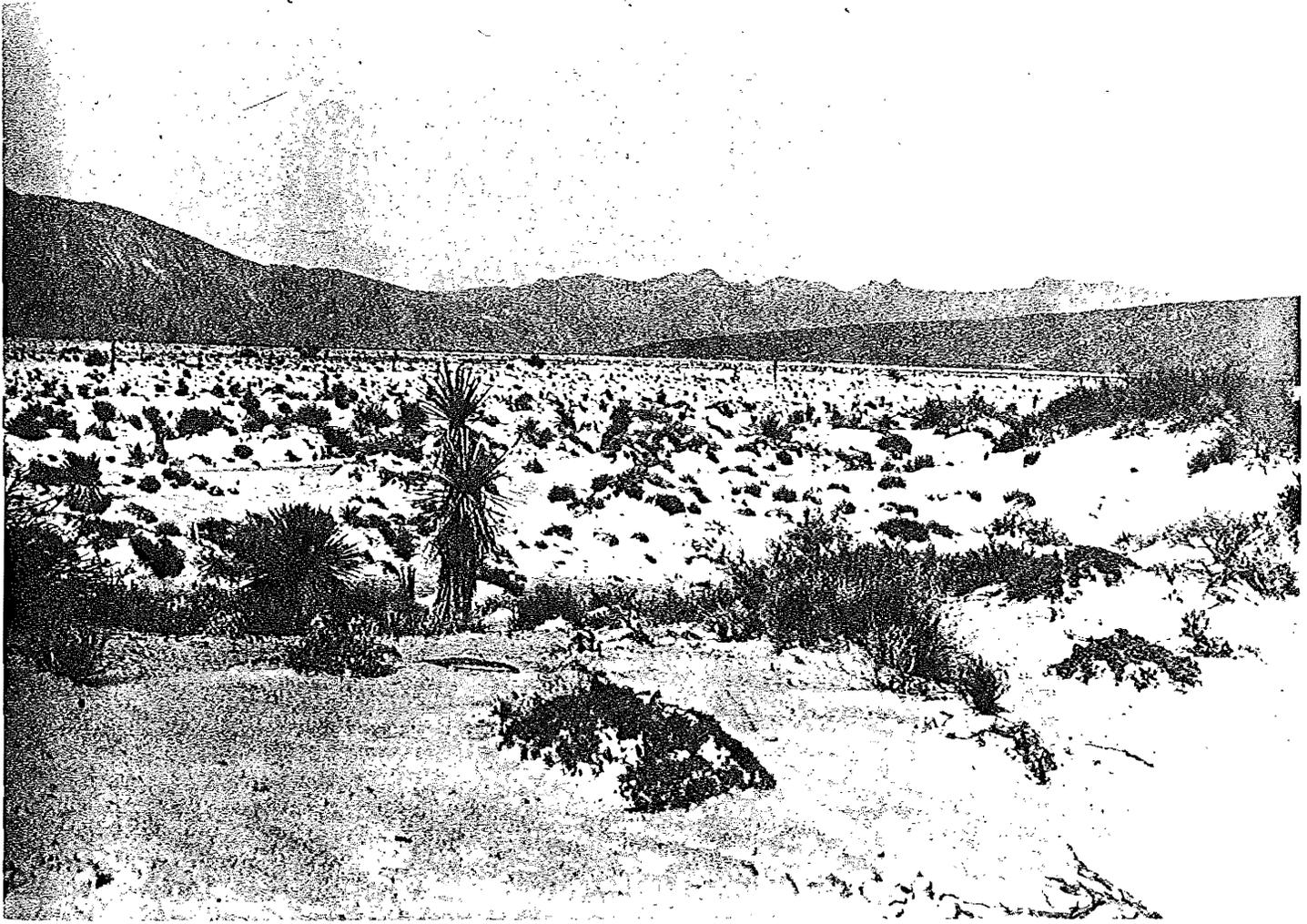


Figure 179. Dune field west of Laguna Grande (see also Fig. 176) in the Cuatro Ciénegas Basin, Coahuila, Mexico. Such dunes of gypsum or other materials are characteristic landscape features downwind of Pluvial lakes and are populated by both gypsophilous-adapted terrestrial and saline-adapted wetland plants. Elevation ca. 750 m.

include *Leptochloa fascicularis* and *L. uninervia*, various *Panicum* spp., *Bouteloua karwinskii*, etc. Herbs, either annual or perennial, are *Allionia incarnata*, *Heliotropium curassavicum*, *Salsola iberica*, *Hoffmanseggia glauca*, and *Tidestromia lanuginosa*, among many others. Aquatic macrophytes are rare. Wigeongrass (*Ruppia maritima*) sometimes becomes dense, but disappears as salinities rise. Other aquatic species (e.g., *Zannichellia palustris* and *Potamogeton pectinatus*) are even more ephemeral, appearing with temporary freshening of these brackish and saline environments.

As along the sea, larger playas have associated dune fields, some of which reflect the special nature of their waters in being of almost pure gypsum (e.g., White Sands, New Mexico, from Pluvial Lake Otero, and dunes in the Cuatro Ciénegas Basin, Coahuila, Mexico; Fig. 179). Under these circumstances, gypsophilous plant species have evolved to complement those especially adapted for existence in saline, interior strand.

Inland playa strands are remarkably inhospitable for animals. Available water is often too salty to drink and plants are

sparse and unpalatable. Black-tailed Jackrabbits (*Lepus californicus*) range into strand to feed when new growth or germination cycles follow freshening. Similarly, seed-eating birds (e.g., Mourning Dove, Black-throated Sparrow, *Amphispiza bilineata*) invade such areas for food, and avoid them when seed production is low [Raitt and Pimm, 1978]. Some marsh and shore birds use these habitats, notably Snowy Plover and Avocet, which are characteristic of alkali playas at inland locales, and large flocks of Sandhill Cranes use Willcox Playa and other shallow water "dry" lakes as wintering ground, along with numerous waterfowl.

Shorelines and grassy flats have a small herpetofauna, principally species of whiptail lizards (*Cnemidophorus* spp.) and their predators such as Whipsnake (*Masticophis flagellum*). Fishes rarely occur, but pupfishes (*Cyprinodon* spp.) occasionally invade and form substantial populations in Laguna Grande and Laguna Salada in Coahuila, Mexico [C. atrorus; Minckley, 1969], or in shorepools as along the Salton Sea [C. macularius; Barlow, 1958].

Tropical-Subtropical Wetlands

Although a number of Tamaulipan elements extend up the Río Grande to beyond Big Bend National Park, only those southwestern wetlands within the Sinaloan and Sonoran biogeographic provinces are considered to belong within this climatic zone (Fig. 3). Even in these provinces the wetland flora and fauna is a mixture of Nearctic and Neotropical species, the former contributing far more to the Sonoran province than to the Sinaloan. As is the case with subtropical uplands, there is a wide range of habitat types, some of which exhibit exceptional plant and animal diversity. Included are consociations of mesquite bosques and palm oases as well as associations of deciduous and evergreen riparian forests, riparian and maritime scrublands, marshland, and strands, and an enormous variety of freshwater, brackish, alkali, and marine submergent communities.

Human alteration of almost all of the regions' rivers coupled with introductions of non-native species has resulted in major modification and displacement of the original stream biota. The relatively few endemic fishes have been reduced in numbers with impoundments

and other stream modifications. These changes in streamflow have been remarkably effective in bringing the large and sometimes bizarre fishes native to the lower Colorado River system to the brink of extinction. Some smaller species persist in good numbers, but other species are becoming increasingly restricted in range. With the passing of the major river also goes a number of delta-dependent fish species from the Gulf of California (e.g., the Giant Totoaba, *Cynoscion macdonaldi*).

It is beyond the scope of this publication to present a discussion of the vast offshore resources of the Gulf of California, although they belong to this thermal zone. A definitive work on the biota of this important marine region is needed. A start in this direction covering reef fishes recently appeared (Thomson et al., 1979). Certainly the abundance and importance of food and game fishes in the Gulf alone warrants such an attempt, and a discussion of its varied migratory and sedentary inhabitants would be most interesting and informative.

Sonoran Riparian Deciduous Forest and Woodlands

Centered in the Sonoran biotic province are streamside associations of tropic-subtropical subspecies of willow [*Salix gooddingii* var. *variabilis*], cottonwood or alamo (*Populus fremontii* var. *macdougalii*), *P. dimorpha*, and/or Velvet Mesquite (*Prosopis velutina*). Winter deciduous, these biomes are nonetheless subtropical riparian where they are restricted to streams and springs below 1,100 to 1,200 m elevation in and immediately adjacent to, the Sonoran Desert. While now much reduced in extent, these forests are still represented by impressive examples and may contain individual trees of great size (Fig. 180).

Willow and cottonwood forests were, and remain, largely restricted to the immediate flood plains of perennial, or at least spring-flowing streams, where they are maintained by periodic winter-spring flooding (Fig. 181). As such, southwestern tropic-subtropical examples are largely restricted to the lower Colorado River and Arizona Upland subdivisions of the Sonoran Desert, which possess watersheds of sufficient winter precipitation and hence the spring discharges necessary to support them. Mesquite "bosques" (Spanish for woodlands) attain their maximum development on alluvium of old dissected flood plains, especially those laid down at the confluence of major watercourses and their larger tributaries (Fig. 182).¹ Consequently, these higher "secondary" flood plains are commonly 1.5 to 6.0 m above the river channel.

Many of the more famous bosques referred to in the literature are today mostly of historical interest—e.g., the mesquite forests at San Xavier, Komatke (New York Thicket), and the mesquite and cottonwood forests along the lower Gila and Colorado rivers. Nonetheless, some excellent examples still occur as scattered remnants along the Santa Maria, Verde, middle Gila, San Pedro, San Miguel, Magdalena, Sonora, and other "desert" river systems. These remaining bosques are, however, all threatened by a variety of human-related causes,—clearing for agriculture and pasture, water diversion, flood control and water storage projects, cutting of trees for fuel, and most importantly, the lowering of groundwater tables. Because mesquite cannot reach groundwater much below 14 m, this last factor has been responsible for the almost total ruin of mesquite forests at San Xavier, Casa Grande Ruins National Monument, Komatke, and elsewhere in Arizona where live streams no longer persist as a result of groundwater pumping. Conversion to agriculture continues to greatly reduce the once extensive bosques along the lowermost Colorado, San Pedro, and Gila rivers. While several thousands of acres of mesquite woodlands have been withdrawn for purposes of preservation, high demands for fuel wood and groundwater threaten all remaining bosques both north and south of the U.S. and Mexican border.

With some notable exceptions, willow-cottonwood forests have been reduced to isolated groves and are now scattered along the Colorado River where they once were extensive [see

¹Although mesquite bosques have been described as occurring in riparian situations within the Mohave and Chihuahuan deserts (e.g. Wauer, 1973), the tall (to over 15 m) tree-forming Velvet Mesquite is lacking in these biomes, mesquite being represented here by the shorter-statured and multi-trunked Western Honey Mesquite (*P. glandulosa* var. *torreyana*), Screwbean (*P. pubescens*) or Texas Honey Mesquite (*P. glandulosa* var. *glandulosa*). Moreover many of the subtropical plants and animal associates of the bosques are lacking in these warm temperate scrublands. Both Fremont Cottonwood and Goodding Willow also occur in warm temperate biomes; again, however, different plants and animal associates are to be expected.

e.g. Ohmart et al., 1977) (Fig. 183). In many places, such areas now are vegetated by *Sonoran riparian scrubland*. Often, the remaining groves are open woodlands of over-mature individuals that are lacking in reproduction and may be expected soon to disappear because of stream regulation. Gallery forest of willow and cottonwood can nonetheless still be found along reaches of undammed and more "natural" portions of the Verde River, middle Gila River, the Hassayampa River below Wickenburg, Arizona, the San Pedro River, and the Río Bavispe and Río Yaqui, all flood-prone ecosystems where Goodding Willow frequently outnumbers cottonwood 100 to 1. Understories may be a tangle of young trees, especially mesquite, or be relatively open.

Historically, annual and perennial grasses (e.g., Vine-mesquite Grass, *Panicum obtusum*), forbs (e.g., Careless Weed, *Amaranthus palmeri*), and in more saline areas, saltbushes (*Atriplex polycarpa*, *A. lentiformis*, *Suaeda torreyana*) constituted the understory in mature bosques. The interior of mesquite bosques was typically open and park-like. Old, fire-scarred trees predominated. Today, because of grazing and other disturbances, a number of introduced forbs and grasses such as Filaree (*Erodium cicutarium*), mustards (Cruciferae), including Yellow Rocket [*Sisymbrium irio*], Red Brome [*Bromus rubens*], and in more open places, Schismus [*Schismus barbatus*] and Bermuda Grass, are frequently encountered understory species. Vines as the climbing milkweeds (*Sarcostemma* spp.), gourds (*Cucurbita* spp.), and Canyon Grape are often common and conspicuous constituents where grazing has not been too severe. Hackberry or Cumero (*Celtis reticulata*), Mexican Elder (*Sambucus mexicana*), and Screw-bean Mesquite may be important arboreal associates, at least locally. At higher elevations (760 to 1,100 m), an individual Velvet Ash [*Fraxinus pennsylvanica* var. *velutina*] or other temperate species, e.g., sycamore, may occupy a particular site, and Blue Paloverde, Catclaw, and Ironwood [*Olneya tesota*] can be common in more arid locations. Graythorn (*Zizyphus obtusifolia*) or one or more of the allthorns [*Lycium fremontii*, *L. andersonii*, *L. berlandieri*] frequently occupy an occasional opening or sunny place along with young mesquites.

The continued clearing of riparian communities along the lower Gila and Colorado Rivers (and in other areas) has resulted in type conversions other than to farmland. It has been noted that where intermittent flooding occurs during the long Southwestern growing season, Saltcedar or Tamarisk [*Tamarix chinensis*] tends to replace mesquite and other native riparian vegetation (Horton, 1977). This tendency is particularly prevalent in saline areas after the native woodlands have been cleared or burned and the water table is at or near the surface. Saltcedar duff is highly flammable and fire initiates a cycle to a disclimax scrub populated only by Saltcedar. Whether this replacement is partially dependent on changes in water and soil chemistry, or entirely a result of the inherent ability of Saltcedar to rapidly repopulate floodplains, is imperfectly known (Everitt, 1980), but the aggressive ability of Saltcedar to displace native riparian species has been well demonstrated by Horton et al. (1960), Turner (1974c), and Warren and Turner (1975). It suffices to say that Saltcedar continues to replace willows, cottonwoods and Mesquite in those bosques where these trees are destroyed, spring floods are controlled, and a saline water table is at or near the surface.

Nesting use of these riparian communities by colonies of White-winged Dove (*Zenaidura macroura*) and Mourning Dove (*Zenaidura macroura*) is well documented (Neff, 1940; Arnold, 1943; Wigal, 1973; Brown, 1977). Their importance to other avian species as Lucy's Warbler, Vermilion Flycatcher (*Pyrocephalus rubinus*), Abert's Towhee [*Pipilo aberti*], Cardinal (*Cardinalis cardinalis*), Pyrrhuloxia [*Cardinalis sinuatus*], Phainopepla, Varied Bunting [*Passerina versicolor*] and others has been discussed by Brandt (1951), Phillips et al. (1964) and more recently by Hubbard (1977b), Anderson et al. (1977), and Clark (1979). Cottonwood-willow forests where they still occur, determine the northern nesting distribution of a number of Neotropical raptors, such as the Gray Hawk (*Buteo nitidus*), in addition to a number of other tropic-subtropical species e.g., Rose-throated Becard and Thick-billed Kingbird (*Tyrannus crassirostris*); these trees also provide nesting sites for the southernmost Bald Eagles. Other localized nesting species are the Yellow-billed Cuckoo, Great Blue Heron, and Mississippi Kite.

Although the few mammals here are not distinctive, numerous bats are characteristic of streamsides in this region. The Silver-haired Bat (*Lasionycteris noctivagans*) and Big Brown Bat (*Eptesicus fuscus*) often roost in trees such as cottonwood. The Desert Pocket Mouse often occupies mesquite bosques as a result of its preference for deep, sandy, rock-free soils (Porter, 1962). Beaver crop cottonwood-willow communities heavily when abundant, and the Raccoon is locally common. It is hypothesized that the former limited occurrence and incursions of Jaguar (*Felis onca*) into Arizona were largely through these subtropical riparian woodlands.

Several other species of tree-requiring vertebrates, such as the Sonoran Spiny Lizard (*Sceloporus clarki*) and Tree Lizard are well represented in riparian woodlands, although not centered there. Open places support whiptail lizards, and some all-female "species" of that complex extend far into deserts along permanent streams. Streamside amphibians other than frogs of the *Rana pipiens* complex, which are common, include the unusual Colorado River Toad (*Bufo alvarius*), a large species that is the scourge of smaller animals in mesquite bosques on rainy summer nights.

The original fish community of the lowermost Colorado and Gila River mainstems was small, consisting of four minnows, two suckers, two or three marine species, a cyprinodontid and a poeciliid. Of these, Woundfin (*Plagopterus argentissimus*), Roundtail Chub, and Flannelmouth Sucker [*Catostomus latipinnis*] were rare, being recorded only a few times in the reach from the present Hoover Dam to the Colorado Delta. The marine Machete (*Elops affinis*) and Striped Mullet (*Mugil cephalus*), and the Desert Pupfish and Sonoran Topminnow (*Poeciliopsis occidentalis*) were only in the lowermost parts of the two rivers (the last only in the Gila). Both of the last species must have inhabited only margins and backwaters. This left a unique assemblage of riverine fishes, consisting only of Colorado Squawfish (*Ptychocheilus lucius*), Razorback Sucker (*Xyrauchen texanus*) and Bonytail Chub [*Gila elegans*], in the main channel of the largest river of the American Southwest.

Backwater sloughs and marshes along the rivers also are known to have been used by Squawfish and Razorback, both of which moved as adults from the channel into such ancillary habitats (Miller, 1961; Minckley, 1965; Seethaler, 1978). Such places also provided refuge areas for protection,

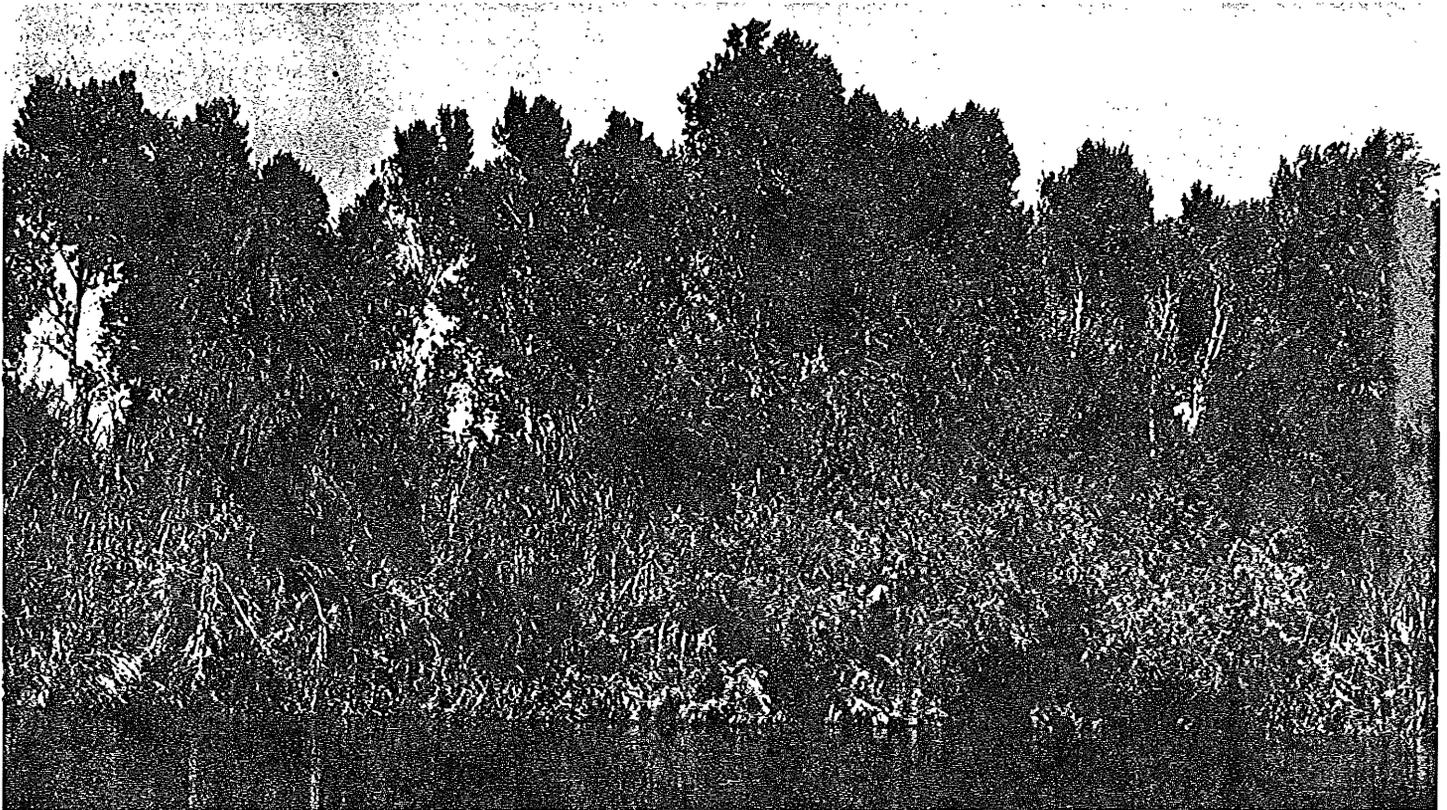


Figure 180. Sonoran riparian deciduous forest of Fremont Cottonwood [*Populus fremontii* var. *macdougalii*] and Goodding Willow [*Salix gooddingii* var. *variabilis*] with Common Reed [*Phragmites australis*] and Saltcedar [*Tamarix chinensis*] at the immediate water's edge. Once extensive, these forests have been reduced to "island" remnants as this one on the Colorado River 20 km west of Yuma, Yuma County, Arizona. Elevation ca. 40 m.



Figure 181. Sonoran riparian deciduous forest of *Populus dimorpha*, *Salix gooddingii*, *Celtis reticulata*, and *Prosopis velutina* along the Rio Yaqui near Highway 15, Sonora, Mexico.

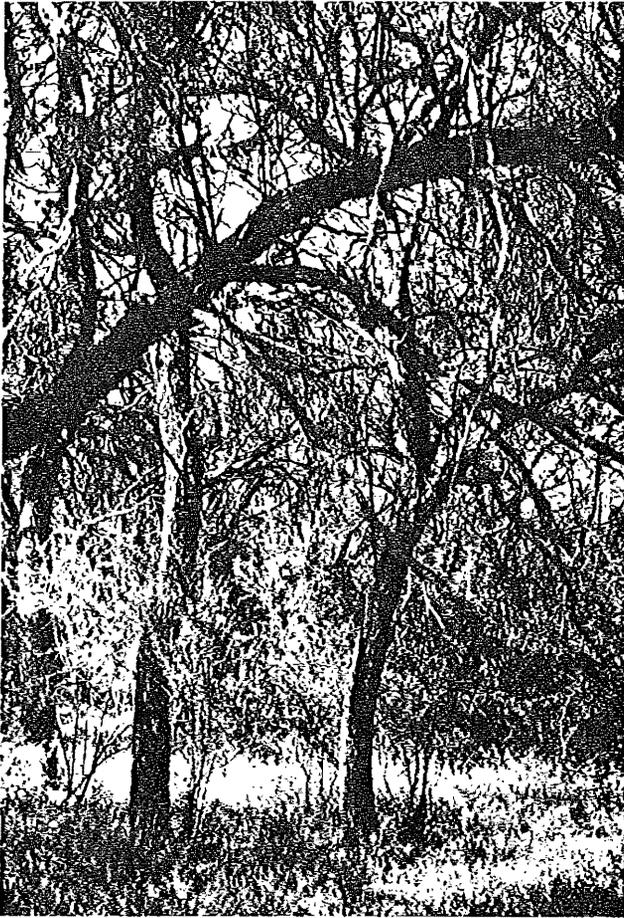


Figure 182. Sonoran riparian deciduous woodland (interior view) - a Mesquite (*Prosopis velutina*) bosque along the San Pedro River near Redington, Pima County, Arizona. Such examples of these magnificent woodlands are becoming rare with declining water tables and increasing demands for cooking and heating fuel. The recent absence of fire is indicated by the abundant presence of young Mesquite. Elevation 900 m.

feeding, and growth by young of these fishes, if such were required, and adults of these and Bonytail Chub used such areas to avoid floods [Minckley, 1973]. All evidence indicates a great abundance of Colorado Squawfish and Razorback Sucker, and that Bonytail were common and widespread [Minckley, 1973, 1979]. These fishes are now almost gone from the area, or in the case of the sucker and Bonytail persist as large adults in reservoirs, with little evidence of successful reproduction.

Minor backwaters, shallows, and shoals over sandbars once available for young native fishes now are occupied by a myriad of introduced predators. Where young squawfish, suckers, or chubs once might have been preyed upon only by water birds such as Great Blue Heron, a host of young Large- and Smallmouth Bass [*Micropterus salmoides*, *M. dolomieu*], lesser sunfishes [e.g., *Chaenobryttus gulosus*, *Lepomis cyanellus*, *L. macrochirus* and *L. microlophus*], cichlids [*Tilapia zilli*, *T. mossambicus*, *T. aureum*], and the voracious Mosquitofish [Meyers, 1965] now occur. The channel and deeper back-

waters are occupied by adults of these species, plus large and specialized predators such as Flathead Catfish [*Pylodictis olivaris*] and Striped Bass [*Morone saxatilis*]. Additional fishes, although perhaps not capable of predation on native forms, certainly increase competitive interactions. Threadfin Shad [*Dorosoma petenense*] feed on plankton and detrital materials, and a bit on benthic invertebrates. Red Shiner [*Notropis lutrensis*] swarms in currents, feeding on drifting and surface materials. Exotic mollies [*Poecilia latipinna* and *P. mexicana*] eat detrital materials and algae. These pressures, accompanied by dewatering of the lower Gila River, channelization which reduced the shallow, quiet backwaters within the strand zone, dredging, and construction of reservoirs and other stabilizing features which enhanced the predominantly lentic-adapted introduced fishes, all have contributed to extinction of this remarkable component of the Southwest's aquatic communities.

Filling of the Salton Sea (Pluvial Lake Cahuilla or LeConte) in 1905-07 by flood flows of the Colorado River, after it broke through frontworks of irrigation channels and was diverted from its normal distributaries to the Gulf of California, created an artificial condition worthy of our treatment.¹ Initially [Evermann, 1916], native fishes from the Colorado River, Bonytail Chub [*Gila elegans*], Razorback Sucker [*Xyrauchen texanus*], Striped Mullet [*Mugil cephalus*], a few trout [*Salmo clarki*], and the introduced Carp were present. Desert Pupfish [*Cyprinodon macularius*] may have entered from the river, or may have spread from springs in the basin that were inundated by rising waters. Machete [*Elops affinis*] appeared later (Dill and Woodhull, 1942).

Evaporative concentration of the Salton Sea gradually increased salinity to exceed seawater (> 35 g/l) in 1945 [Carpelan, 1961], perhaps accelerated by diversion of saline irrigation return waters to the basin. Freshwater fishes disappeared prior to the 1950s, with the exception of Pupfish; marine fishes also failed to reproduce and began to disappear. From 1929 through the late 1940s, numerous invertebrates and fishes were introduced in an attempt to create an inland marine fishery, but by 1949, only pupfish, Mosquitofish, a few Striped Mullet and Longjaw Mudsucker [*Gillichthys mirabilis*] remained. After 1950, introductions of Sargo [*Anisotremus davidsoni*], Bairdiella [*Bairdiella icistius*], and predatory Orangemouth Corvina [*Cynoscion xanthulus*] spawned successfully [Walker et al, 1961]. This fishery persists today, but introductions of numerous salt-tolerant freshwater fishes such as Red Shiner, African cichlids [*Tilapia mossambicus*, *T. zilli* and others], and a myriad of Central American poeciliids [*Poecilia latipinna*, *P. mexicana*, *Poeciliopsis gracilis*, *Xiphophorus variatus*, *X. helleri*] is now endangering the native

¹This situation obviously happened before, since Wilke (1980) has demonstrated that a Neolithic fishing culture existed on the shores of the Cahuilla Basin ca. 1,500 years before present. Rock wiers were constructed annually along shorelines to intercept aggregations of Razorback Sucker and Bonytail Chub, both of which were recovered from middens in the area. Wiers were progressively constructed downslope, at a rate commensurate with projected annual evaporative decline in water levels, and the fishery collapsed in about 55-60 years, at a time when salinities would likely have resulted in decreased populations of freshwater fishes.



Figure 183. Riparian deciduous forest of cottonwood [*Populus fremontii* var. *macdougalii*] along the Colorado River near Yuma, Yuma County, Arizona, near the turn of this century. The river and its magnificent riparian ecosystem are still "untamed" as construction of the Imperial Canal is underway. Elevation ca. 100 m. Photograph courtesy of the U.S. Bureau of Reclamation and Robert D. Ohmart.

pupfish (Schoenherr, 1979) and the valuable game fishes as well.

The few, smaller streams of lowlands draining into the Gila River once supported a simple community of Longfin Dace, Sonoran Topminnow, and occasionally Desert Pupfish. Pupfish populations now are extinct throughout the vast basin, and are approaching extinction in the Río Sonoyta in northern Sonora as a result of pumping along that stream; a remnant is protected at Organ Pipe Cactus National Monument in Quitobaquito Spring. The Sonoran Topminnow has been destroyed in the Gila River basin except for a few populations in springs, isolated stream segments, or artificial refugia (Minckley et al., 1977); however, as noted above, it remains abundant in the Río Yaqui and lesser drainages of northwest Sonora.

Coastal rivers between the Colorado and Río Yaqui generally enter sands at their lower reaches before entering the sea; their fauna is thus restricted to middle and highland portions. Longfin Dace is the only species that has succeeded in occupying all these desert rivers, from the Río Sonora to the Río Sonoyta; Sonoran Topminnow is found in all but the latter stream. The Yaqui Chub [*Gila purpurea*] occurs in the ríos Matape and Sonora along with Mexican Stoneroller. The Opata Sucker [*Catostomus wigginsi*] is restricted to Río Sonora and Sonora Chub [*Gila ditaenia*] holds forth in the Río Concepción. Desert Pupfish is shared by Río Sonoyta and the lower Colorado-Gila rivers, reflecting in its presence the intimate relationships of the first stream to the Colorado River delta prior to its diversion south by the Pinacate lava flows (Hubbs and Miller, 1948).

Sonoran Oasis Forest and Woodlands

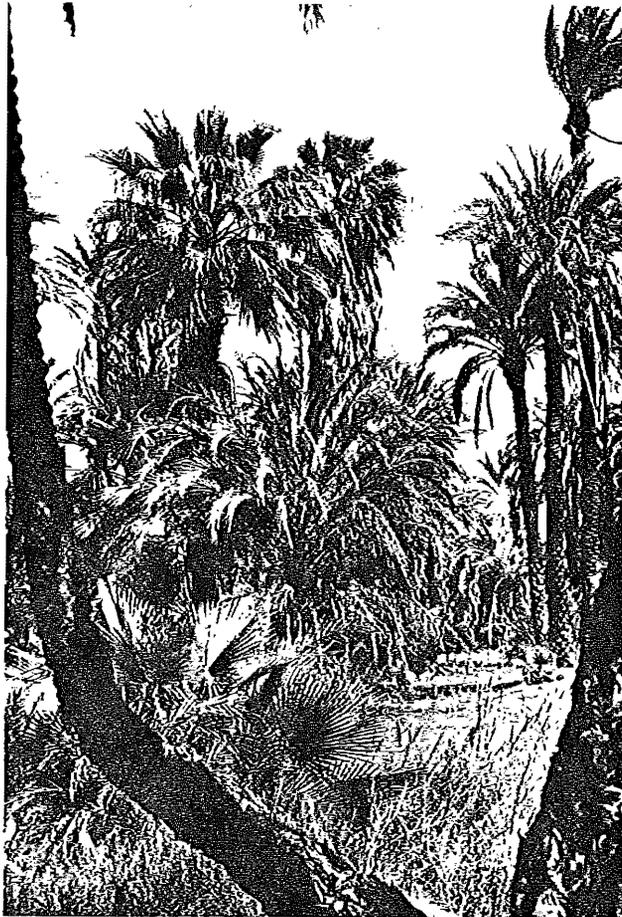


Figure 184. Sonoran oasis of native California Fan Palms [*Washingtonia filifera*] and feral Date Palm [*Phoenix dactylifera*] at San Ignacio, Baja California del Sur, Mexico. Elevation ca. 250 m.

These evergreen, Miocene and Pliocene relicts are restricted to certain isolated, permanent springs, seeps and moist canyons, in and at the western edge of the Sonoran Desert. In Arizona and California, natural oases are represented by groves of the California Fan Palm [*Washingtonia filifera*], and in Baja California del Norte by California Fan Palm and/or Blue Fan Palm [*Erythea armata*]. Further south in Baja California, the Sky-duster Palm [*Washingtonia robusta*] makes its appearance as do feral populations of Date Palm [*Phoenix dactylifera*]. The last species now dominates the oases at Mulegé and San Ignacio and has so for many years [Shreve, 1951; Moran, 1977; Fig. 184].

Although numerous localities for *Washingtonia filifera* have been reported for California and Baja California del Norte, the only native palms in Arizona are those in the Kofa Mountains, at and near Alkali Springs near Castle Hot Springs, and possibly at Ciénega Spring northeast of Parker. This is the palm of such famous southern California oases as Palm Springs, 29 Palms, and Palm Desert. There it grows both in arroyo habitats and at seeps, particularly those along the San Andreas fault zone(s) [Vogl and McHargue, 1966]. In many places, the groves have been destroyed; yet this species has been introduced and cultivated to the extent that it is an ubiquitous ornamental throughout the Southwest's subtropical and warm-temperate regions.

Blue Palms are endemic to northern Baja California [including Isla de la Guarda]; one population on the eastern slope of the Sierra Juarez is within 24 km of the International Boundary [Moran, 1977]. This species is also found in arroyo habitats where it is frequently accompanied by California Fan Palms.

Neither *Washingtonia* nor *Erythea armata* occur naturally in Sonora. Groves of the Mexican Blue Palm [*Sabal uresana*] and *Erythea aculeata* within and near Sinaloan thornscrub in that state are perhaps best considered as northern consociations of Sinaloan riparian mixed evergreen forest.

Plant associates are the more mesic and riparian species found within the Sonoran desert. Except for Fremont Cottonwood, the associates are of considerably shorter stature than the palms. Some common residents in fan palm oases in California and Arizona according to Vogl and McHargue (1966) and Brown et al. (1976) are:

<i>Acacia greggii</i>	<i>Cynodon dactylon</i>
<i>Ambrosia ambrosioides</i>	<i>Hymenoclea monogyra</i>
<i>Atriplex</i> spp.	<i>Phragmites australis</i>
<i>Baccharis salicifolia</i>	<i>Prosopis velutina</i>
<i>Baccharis sarothroides</i>	<i>Tamarix chinensis</i>
<i>Carex ultra</i>	<i>Tessaria sericea</i>
<i>Cercidium floridum</i>	<i>Zizyphus obtusifolia</i>

California Fan Palms are alkali tolerant and, once established, appear to increase or maintain themselves against potential competitors if water supplies are adequate.

No vertebrate species are known to be exclusively associated with these communities, but the presence of dense foliage and moisture in the arid environments undoubtedly enhances and concentrates local animal inhabitants. Ryan [1968] speculated that the rare occurrence of the Western Yellow Bat [*Dasypterus egaxanthinus*] in the southwestern United States was closely associated with palm oases.

Sinaloan Riparian Evergreen Forest and Woodland

These diverse tropic-subtropical streamside communities extend northward into our area to as far north as the lowermost Río Yaqui and its tributaries. There, at their northern extremity, they are mostly below 760 m elevation, but may extend to as high as 1,100 or 1,500 m farther south in the region around Alamos [Gentry, 1942; Felger, 1971]. Contained within subtropical deciduous forest and thornscrub, the contrast in winter between these evergreen and semi-evergreen bottomland communities with adjacent, bare hillsides is striking.

Overstory species include a number of stately, tropic-subtropical trees, occurring alone or as mixtures (Figs. 185, 186). In the Southwest, these include several species of wild figs (*Ficus* spp.), a cottonwood (*Populus dimorpha*), Goodding Willow, palms (*Sabal uresana*, *Erythea aculeata*, *Clethra lanata*), and the stately Montezuma Cypress or Cedros (*Taxodium mucronatum*); overstories may be closed (forest) or open (woodland). At higher elevations several warm temperate trees, such as sycamore, the Evergreen Magnolia (*Magnolia schiediana*) and oaks may join the forest assemblage (Felger, 1971). Lianas (*Arrabidaea litoralis*, *Marsdenia edulis*, *Gouania mexicana*) and the climbing *Pisonia capitata* increase diversity. Tropical epiphytes are represented by the orchid *Oncidium cebolleta* and bromeliads (e.g., *Tillandsia inflata*, *Hechtia* spp.). A characteristic understory shrub is Garabato (*Celtis iguanaea*). Other understory species according to Gentry [1942] and Felger [1971] are:

<i>Bacopa monnieri</i>	<i>Prosopis juliflora</i>
<i>Begonia</i> spp.	<i>Rotala ramosior</i>
<i>Eustoma exaltatum</i>	<i>Samolus ebracteatus</i>
<i>Fuirena simplex</i>	<i>Sartwellia mexicana</i>
<i>Gratiola brevifolia</i>	<i>Sassafridium macrophyllum</i>
<i>Guazuma ulmifolia</i>	<i>Selaginella</i> spp.
<i>Heteranthera limosa</i>	<i>Sesbania sesban</i>
<i>Oreopanax salvinii</i>	<i>Stanhopea</i> spp.
<i>Pithecellobium</i> spp.	<i>Vallesia glabra</i>
	<i>Vitex mollis</i>

These communities host a large and varied animal community. This fauna has been poorly investigated but includes such large and spectacular species as the Jaguar and the smaller Ocelot (*Felis pardalis*). Heteromyid rodents (*Dipodomys* spp. and *Perognathus* spp.) are common in the region but not particularly characteristic of riparian zones. Cotton rats (*Sigmodon hispidus*, *S. minimus*) tend to be more abundant near streams and other wetlands, and troops of Coati (*Nasua nasua*) forage extensively within the riparian corridors [Burt, 1938].

Birds include the spectacular Military Macaw [*Ara militaris*], Black-bellied Tree Duck [*Dendrocygna autumnalis*], and Magpie Jay [*Calocitta formosa*]. Other colorful species are the Lilac-crowned Parrot (*Amazonia finschi*), Blue-rumped Parrotlet (*Forpus cyanopygius*), Green Parakeet [*Aratinga holochlora*], Coppery-Tailed Trogon, Berylline Hummingbird (*Amazilia beryllina*), Black-chinned Hummingbird [*Archilochus alexandri*], the unique Russet-crowned Motmot (*Momotus mexicanus*), and a host of songbirds and other species more typical of riparian communities to the north (e.g., Gila Woodpecker, *Melanerpes uropygialis*; Van Rossem, 1945).

Reptiles and amphibians of these communities are rich and diversified—73% of the overall fauna of 74 species recorded



Figure 185. Sinaloan riparian evergreen woodland of Montezuma Cypress (*Taxodium mucronatum*) on the Río Cuchajaqui, a tributary of the Río Fuerte, near Alamos, Sonora, Mexico. Elevation ca. 760 m.

from near Alamos, Sonora, had northern affinities and the remainder was from the tropics (25%) or endemic to Mexico (2%). Unfortunately, Heringhi (1969), who detailed the herpetofauna, did not provide critical information on habitat relations, but amphibians associated with watercourses certainly include Colorado River Toad, Giant Toad (*Bufo marinus*), a tree-frog (*Pachymedusa dacnicolor*), and Leopard Frog. Turtles, too, are far more common in this area than elsewhere in the Southwest. Mud turtles (*Kinosternon hirtipes* and *K. integrum*, *K. alamosae*), although semi-aquatic, are frequent in streams and arroyos, and larger waters support the pond turtles *Chrysemys picta*, *Pseudemys scripta mayae*, and *Rhinoclemmys pulcherrima*. Snakes directly associated with the water are Boa Constrictor (*Constrictor constrictor*), Watersnake (*Natrix valida*), and Indigo Snake (*Drymarchon corias*); others are associated with streamside trees (Vine Snake, *Oxybelis aeneus*), with fine soils on stream terraces (Blackhead Snake, *Tantilla planiceps yaquiae*), or are attracted to mesic habitats.

Creeks and rivers of the southern Río Yaqui drainage at lower elevations, and the Río Mayo to the south, support tropical fishes capable of dispersing through brackish water, e.g., Pacific Shad (*Dorosoma smithi*), topminnow (*Poeciliopsis prolifica*), and the all-female *P. monacha-occidentalis* that depends on sperm of bisexual species of *Poeciliopsis* for its unique forms of reproduction (gynogenesis and "hybridogenesis"; Schultz, 1977), and, where pools are present, Sinaloan Cichlid (*Cichlasoma beani*). Forms such as Mexican Stoneroller, Longfin Dace, and in the Río Yaqui proper, Beautiful Shiner, Yaqui Sucker, Yaqui Catfish (*Ictalurus pricei*), and Roundtail Chub, all enter this tropical zone, which approaches to southern limits of natural range for most of these northern genera on the west coast of Mexico (Meek, 1904; Miller, 1959; Stuart, 1964). Marine fishes penetrate these lowland rivers far above tidal influence. A goby (*Awaous transandeanus*) has been taken near Movas and almost to Presa Novillo on the Río Yaqui, and Mountain



Figure 186. Rio Chico near the town of Rio Chico, Sonora, Mexico. Cottonwood [*Populus monticola*], willow [*Salix spp.*], wild fig [*Ficus spp.*] and thornscrub [*Acacia spp.*] as a mixed riparian community along the boulder-bottomed stream. Elevation ca. 200 m; photograph by Dean A. Hendrickson, June 1978.

Mullet [*Agonostomus monticola*] also has such capability [Hendrickson et al., 1981]. Introduced species such as Largemouth Bass, White Crappie [*Pomoxis annularis*], Bluegill [*Lepomis macrochirus*] and Redear Sunfish [*L. microlophus*]

are generally restricted to reservoirs, but the stream-adapted Carp [*Cyprinus carpio*], River Carpsucker [*Carpoides carpio*], and Green Sunfish [*Lepomis cyanellus*] have invaded and become established in local creeks and rivers.

Sonoran Riparian Scrubland

In and along drainages within the Sonoran Desert are scrublands of low to medium height (1.5 to 3.0 m), too dense to be considered desertscrub or strand. Although these scrublands usually contain plant species also found in adjacent desertscrub (e.g., *Lycium brevipes*, *Acacia greggii*, *Celtis pallida*, and especially the highly facultative mesquite), the actual stream channel dominants are usually distinctive riparian species. Seepwillow (*Baccharis salicifolia*) is abundant nearest water, with Desert Broom (*B. sarothroides*) in drier places and Mule Fat (*B. viminea*) in desert washes. Arrow-weeds (*Tessaria sericea*, *Pluchea camphorata*, and *P. purpurascens*) and Burro-

brush may dominate on sandy soils (Fig. 187). These and other evergreen shrubs have adapted to successional situations as befits their restricted occurrence to flood-prone areas. The deciduous Desert-willow (*Chilopsis linearis*) is a common arboreal component, as is the increasingly prevalent, deciduous Saltcedar.

Along the saline portions of the lower Colorado and Gila rivers and in the Salton Sea basin, are dense and taller (to 11 m or higher) "thickets" of introduced Saltcedar and the evergreen Athel (*Tamarix aphylla*). In the less disturbed sites, these may be accompanied by native Screwbean Mesquite, Lenscale, or Quailbush (*Atriplex lentiformis*), Arrow-weed, Western Honey Mesquite (*P. glandulosa* var. *torreyana*), and such purely salt-shrub species as *Suaeda torreyana*, *Atriplex polycarpa* and *Allenrolfea occidentalis* (Fig. 188). These communities are highly flammable because of deciduous and other properties of Saltcedar, and are now typically in a fire-succession stage. Each fire (or clearing) increases the prevalence of the root sprouting Saltcedar at the expense of more valuable native vegetation. Consequently, fire disclimax consociations of Saltcedar now exclusively occupy extensive areas along the lower Colorado River, its delta, tributaries, distributaries (e.g., Río Hardy, Alamo, and New rivers), agricultural drains and sumps, and other poorly-drained, alkaline places (Fig. 189).

The value of these thickets to game species is well known, and such places often support a high density of Desert Cottontail (*Sylvilagus auduboni*) and Gambel's Quail (*Lophortyx gambeli*), and if of sufficient height (3+ m), nesting Mourning and White-winged Doves. Other birds well represented in Sonoran riparian scrub are the Crissal Thrasher, Abert's Towhee, Brown Towhee (*Pipilo fuscus*), Say's Phoebe (*Sayornis saya*), and Black-tailed Gnatcatcher (Anderson and Ohmart, 1977; Anderson et al., 1977). If standing water is present, such scrublands may also often be inhabited by the Yuma Clapper Rail (*Rallus longirostris yumaensis*).



Figure 187. Sonoran riparian scrubland, strand, and woodland on the Verde River, Tonto National Forest, Maricopa County, Arizona. Scrubland composed largely of Burrobush (*Hymenoclea monogyra*), Arrowweed (*Tessaria sericea*) and Velvet Mesquite (*Prosopis velutina*) in scrub form. Elevation ca. 450 m.



Figure 188. Sonoran "lower Colorado River" scrub of Arrowweed [*Tessaria sericea*, *Pluchea camphorata*], Saltcedar (*Tamarix chinensis*), Western Honey Mesquite [*Prosopis glandulosa* var. *torreyana*], Screwbean (*Prosopis pubescens*), Lenscale or Quailbush [*Atriplex lentiformis*] and Seepweed [*Suaeda torreyana*], with an occasional willow [*Salix exigua*, *S. gooddingii*], near Cibola, Yuma County, Arizona, along the Colorado River. Elevation ca. 120 m.

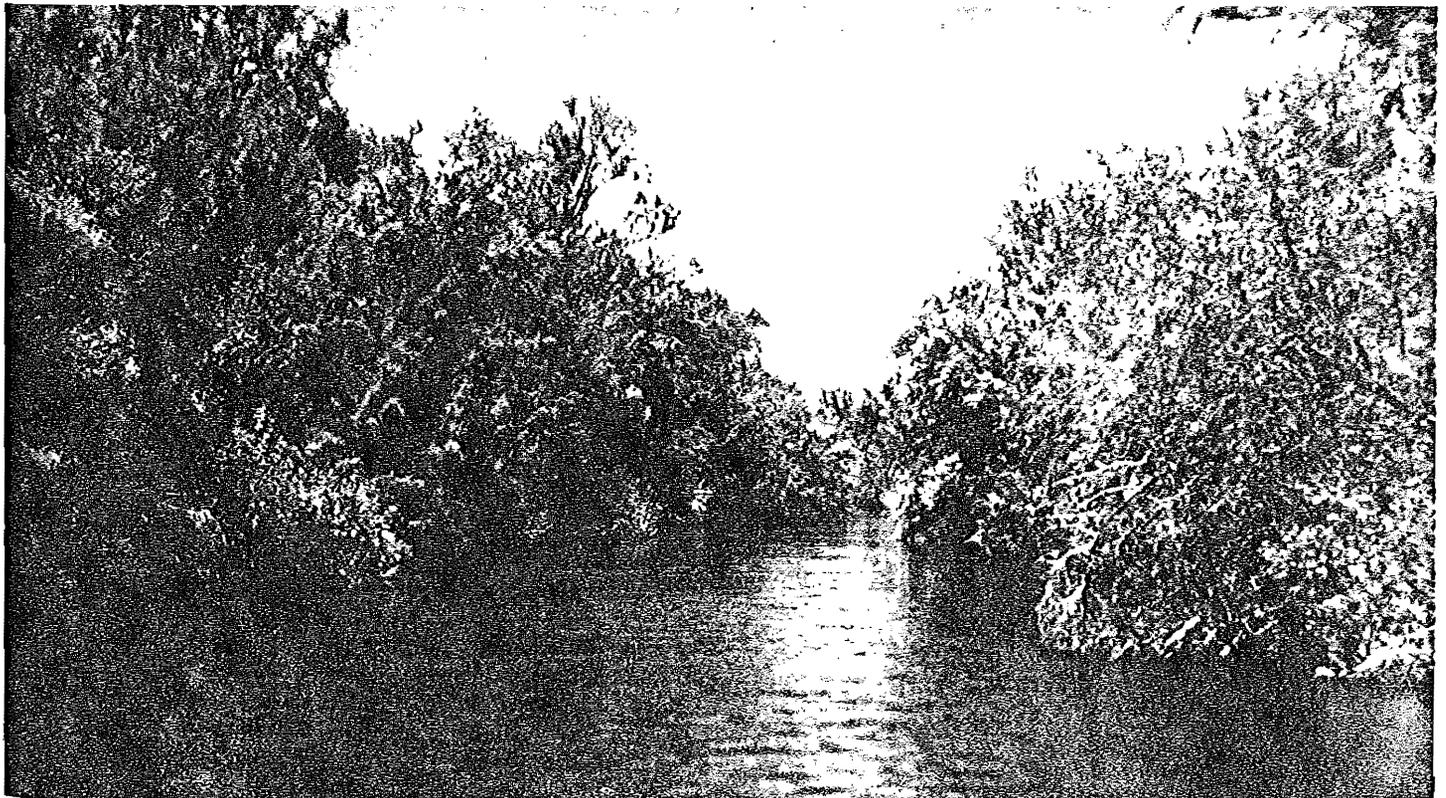


Figure 189. Sonoran "lower Colorado River" riparian scrub in the Colorado River delta below Riito, Sonora, Mexico. A disclimax community dominated by Saltcedar (*Tamarix chinensis*). The remaining few mesquites [*Prosopis glandulosa* var. *torreyana*, *Prosopis pubescens*] will eventually be displaced with increasing incidence of fire brought on by the flammable properties of Saltcedar. Elevation ca. 5 m.

Sinaloan Maritime Scrubland

Mangrove swamps of considerable extent occur in the Boca del Yaqui region of the Sonoran Coast, i.e., from due south of Ciudad Obregón to west of Potám. Other small, discontinuous areas are in protected bays, lagoons, and estuaries on the coast northward to near Punta Sargento [29° 18'N] and on the Gulf Coast of Baja California northward to just south of Bahía de Los Angeles [29° 05'N] (Felger and Lowe, 1976). Mangroves are rare or absent north of 27°00'N on the Pacific side of Baja California (Hastings et al., 1972).

Species present may be all or any of Black Mangrove (*Avicennia germinans*), Red Mangrove (*Rhizophora mangle*), and White Mangrove (*Languncularia racemosa*). The lack of other plant associates is often conspicuous, and delineation of these tideland communities is abrupt, with little integration with adjacent strand, tidemarsch, and/or desertscrub (salt-bush) communities (Fig. 190, 191).

As many of their names imply, several bird species are closely associated with Sinaloan maritime scrub—the Mangrove Cuckoo (*Coccyzus minor*), Mangrove Swallow (*Iridoprocne albilinea*), Mangrove Warbler (*Dendroica erithachorides*), and others such as Tiger Bittern (*Tigrisoma mexicanum*), Wood Stork (*Mycteria americana*), Anhinga (*Anhinga anhinga*), and Roseate Spoonbill (*Ajaia ajaia*). Two particularly abundant nesting birds in mangrove swamps are White-winged Dove and Clapper Rail.

The value of these wetlands as nurseries and feeding grounds to a host of marine life is well known. Juveniles and young adults of commercial and sport fishes are common, e.g., snappers (*Lutjanus* spp.). The Giant Jewfish (*Epinephelus itajaro*), which may achieve weights of 450 kg in open waters of the Gulf, occurs as young only in mangrove-vegetated esteros (Thomson, 1973).



Figure 190. Sinaloan maritime scrubland and "barrier" strand bordering the Sonoran Desert, Sonora, Mexico. A northern outlier of the more extensive mangrove swamps farther south at Punta Sargento, this scrubland is composed mainly of Black Mangrove (*Avicennia germinans*). Photograph by Richard L. Todd.



Figure 191. Interior view of Sinaloan maritime strand and scrubland near Punta Sargento, Sonora, Mexico. Note the "chapparal-like" landscape physiognomy and simplicity in overstory species composition (*Avicennia germinans*).

Sonoran and Sinaloan Interior Marshlands and Submergent Communities

Freshwater marshes are rare in these biogeographic provinces. This is because of their dependence on old oxbows of large rivers as the Colorado, Yaqui, Mayo, etc. Today, many of the larger marshlands occur where rivers enter large reservoirs (e.g., the "delta" of the Bill Williams River in Lake Havasu, Arizona). A very few are associated with natural springs or intersect groundwater tables, the last as at Laguna Prieta (Fig. 151). More common today are brackish and saltwater marshlands dependent for their existence on wastewater discharges, agricultural drains, and silt-laden reservoirs. These include the managed marshes at the edges of the Salton Sea in Imperial County, California, Santa Clara Slough near the Gulf of California, and Picacho Lake in Pinal County, Arizona.

Emergent vegetation varies from pure stands (=consociations) of such short statured and alkali resistant species as Saltgrass, Alkali Bulrush (*Scirpus maritimus* var. *paludosus*), and Three-square (*Scirpus americanus*), to dense, impenetrable communities of reed (*Phragmites australis*) and Giant Bulrush (*Scirpus californicus*), locally called "tules." Often, however, the most prevalent and characteristic species is the cattail, principally represented in these parts of the Southwest by *Typha domingensis*. At the edge of the marsh there is typically much intermingling with adjacent scrublands of Saltcedar, Arrow-weed, Quailbush (*Atriplex lentiformis*), and mesquite [Fig. 192]. In more seasonally flooded areas the communities are often mosaics of the shorter marsh species (i.e., *Juncus* spp., *Eleocharis* spp., *Cynodon dactylon*, *Distichlis spicata*) and taller scrub (e.g., Saltcedar) depending on slight variations in hydrology or successional stage. As with all marshlands, hydrosol mud bottoms are characteristic.

Emergent aquatic vegetation along the channel of the now stabilized Colorado River mainstream includes larger sedges such as Giant Bulrush and Three-square (Minckley, 1979). These plants form thick stands which rise as high as 3 m above the surface, creating a broad, 1-5 m zone of quiet, shaded water to 1.5 m deep. Cattail also forms beds on sloping, stabilized or aggrading banks that extend as far as 15 m from shore in water to a meter deep, especially on the quiet side of bends. When currents contact such beds, dense roots and rhizomes hold as dense mats, and undercuts of more than 2.5 m may occur. Stands of Giant Reed also are present, living as large clumps along less hygric shorelines.

Numerous small, semi-aquatic plant taxa form understories within marsh communities and along the banks. Included here are Pennywort (*Hydrocotyle verticillata*), Water-hyssop, Smartweed (*Polygonum fusiforme*), Spearmint (*Mentha spicata*), and a diversity of sedges and grasses (*Cyperus strigosus*, *C. erythrorhizos*, *Eleocharis parvula*, *E. caribaea*, *Leptochloa uninervis*, and *Paspalum dilatatum*).

Present-day submergent communities of the lower Colorado River channel are obviously new since drastic fluctuations in water levels and scour prior to dams scarcely allowed their development in more than a periodic or rudimentary way. Today there are large, monospecific stands of Sago Pondweed (*Potamogeton pectinatus*) with Water Milfoil (*Myriophyllum spicatum*) and the introduced Parrot-feather [*M. brasiliense*] collectively second in abundance (Minckley, 1979). The pondweed is most common in deeper water [to 4.5 m] and often in current that exceeds a meter per second. Milfoil and Parrot-feather form dense beds in shallower [to 2.5 m] water that moves at less than 0.5 m/second. Charophytes are in eddies or other places with slower currents, but are also interspersed with other taxa in the channel. Shorelines and quiet backwaters support some Hornwort (*Ceratophyllum demersum*), but more commonly these areas are choked with Holly-leaved Naiad (*Najas marina*). Shallow waters are inhabited by stands of Leafy Pondweed (*Potamogeton foliosus*), Common Pondmat (*Zannichellia palustris*), and sparse stands of Water Nymph [*Najas guadalupensis*]. Bladderwort (*Utricularia* spp.) and duckweeds (*Lemna* spp.) commonly inhabit quiet backwaters, and often are entangled with other plants in the channel.

Although these marshlands and aquatic communities are justifiably considered important wintering grounds for water-



Figure 192. Topock Marsh, an interior marshland on the Colorado River at the northernmost edge of the Sonoran Desert, Mohave County, Arizona. The cattail is *Typha domingensis*; the shrub in foreground is *Atriplex lentiformis*. Elevation ca. 260 m; photograph by Richard L. Todd.

fowl, they also possess (or possessed) a distinctive nesting avifauna, some distinctly Neotropical. Examples of the latter are Fulvous Whistling Duck (*Dendrocygna bicolor*), Purple Gallinule (*Porphyryla martinica*), Least Grebe (*Podiceps dominicus*), and Snowy-egret (*Egretta thula*). Other species such as Sora, Coot (*Fulica americana*), Black-crowned Night Heron, Least Bittern (*Ixobrychus exilis*), Red-winged Blackbird, and Yellow-throat are widespread species in both temperate and tropical North America. Nesting populations of the Yuma Clapper Rail, a fresh- or brackish-water race of the species, are restricted to spring-wet Sonoran marshlands along the Colorado River, and in more interior locales whenever several hectares of marsh vegetation approaches or exceeds a meter in height.

The Muskrat (*Ondatra zibethicus*) is the common mammalian inhabitant, foraging on vegetation and on the now abundant, introduced Asiatic Clam (*Corbicula fluminea*). The Sonoran Mud Turtle [*Kinosternon sonoriense*] and other mud turtles are still locally common, as are the Colorado River and Giant Toads [*Bufo alvarius*, *B. marinus*] within their respective ranges. Nonetheless, the former distribution of the Sonoran Mud Turtle once included the lowermost Colorado and Verde

rivers where it now is rare or absent, possibly replaced by the Spiny Softshell Turtle, introduced into the Colorado River at around the turn of the century (Miller, 1946). Another introduction, the Bullfrog (*Rana catesbeiana*), is now widespread throughout many mudbottomed, freshwater habitats within the Sonoran and Sinaloa provinces, where it contributes to the present day rarity of the native Checkered Garter Snake (*Thamnophis marcianus*; see also Moyle, 1973 and Conant, 1978), and at least locally, native frogs.

Populations of small fish species, such as Desert Pupfish and Sonoran Topminnow, now are extirpated from much of their former ranges in this zone because of interactions with introduced fishes and dewatering of streamside marshes. Salton Sea agricultural drains and a few spring-fed marshes still support small numbers of the pupfish, but African cichlids and a myriad of other, tropical fishes [e.g., Sailfin and Mexican Mollies, *Poecilia latipinna* and *P. mexicana*] now threaten even these refugia. These non-native forms also are present along the lower Colorado River and are exerting inexorable pressure; the pupfish remains common only in hypersaline parts of Santa Clara Slough on the Colorado River Delta.

Sonoran Maritime Strand and Submergent Communities

Both the Baja California and Sonora coasts of the Gulf of California possess tide flat, beach dune, beach rubble, and sea cliff habitats. The mud substrates of the quieter waters may be inhabited by tide-influenced communities of Iodine Bush (*Allenrolfea occidentalis*), Seepweed, Sea-lavender (*Limonium californicum*), saltbushes (*Atriplex barclayana*, and others), Batis (*Batis maritima*), alkali-heath (*Frankenia* spp.), Ice Plant, glassworts (*Salicornia* spp.), Saltgrass, and other halophytes (e.g., *Tricerma phyllanthoides*). The plant cover varies from almost nil to open to relatively dense tidalscrub, and is dependent on frequency of inundation and edaphic conditions (Felger and Lowe, 1976). The upper, inland associations commonly grade into desertscrub and there may be much intermingling of the two, both in aspect and composition. Beach dunes are normally thinly vegetated, if at all, by deep-rooted, mat-like, or otherwise short-statured forbs, grasses being poorly represented on these subtropical beaches (Fig. 193). Examples given by Felger and Lowe (1976) of strand vegetation on dunes along the Sonora coast are: *Abronia maritima*, *A. villosa*, *Astragalus magdalenae*, *Dicoria canescens*, *Euphorbia leucophylla*, *Monanthochlœ littoralis*, *Jouvea pilosa*, *Helianthus niveus*, and *Croton californicus*. As elsewhere, the lateral dunes closer to the sea are more subject to wind and spray and so, possess less vegetative cover. The beaches themselves are essentially free of vegetation.

Even harsher environments for plants are rock rubble and sea cliff shores. The vegetation on these sites is typically extremely sparse and may be composed of nonvascular species, annuals and/or the hardier cliff-dwelling desertscrub and thornscrub perennials found inland. Examples, again from Felger and Lowe (1976), are: *Amaranthus watsonii*, *Nicotiana trigonophylla*, *Ficus petiolaris*, *F. palmieri*, *Hofmeisteria crassifolia*, *H. fasciculata*, *Eucnide rupestris*, *Pleurocoronis laphamoides*, and the Sweet Mangle (*Maytenus phyllanthoides*).

Rocky coastal environments are sometimes the hauling sites for large herds of California Sea Lions. While the sand "hauling" beaches used by Green Sea Turtle are now rare, sandy beaches and mud flats provide winter feeding habitats for migrating curlew, sandpipers, dowitchers, phalaropes, and other shore birds. Nesting species using these habitats are often restricted to islands (e.g., Isla Raza) and some of the less disturbed mainland beaches. These include the Royal Tern (*Thalasseus maximus*), Elegant Tern (*T. elegans*), Least Tern, Snowy Plover, and Wilson's Plover (*Charadrius wilsonia*). Rocks and sea cliffs, especially on offshore islands, often host such colonial nesting pelagic and shore foraging birds as the Manx Shearwater (*Puffinus puffinis*), Western Gull (*Larus occidentalis*), Heermann's Gull (*L. heermanni*), Laughing Gull (*L. atricilla*), Brown Booby (*Sula leucogaster*), Blue-footed Booby (*S. nebouxii*), Blue-faced Booby (*S. dactylatra*), Least Storm Petrel (*Halocryptena microsoma*), Black Storm Petrel (*Oceanodroma melania*), Brown Pelican (*Pelecanus occidentalis*), Double-crested Cormorant, Black Skimmer (*Rynchops nigra*), and Red-billed Tropicbird (*Phaethon aethereus*). Other more solitary and habitat specific nesting species include the American Oyster Catcher (*Haematopus pallitus*) (rock rubble), and Osprey (*Pandion haliaetus*) (pinnacle or other elevated structure).

Fish communities of the intertidal (littoral) zone of the Gulf of California have recently been discussed by Thomson et al. (1979). In the upper Gulf, above the "midriff" islands of

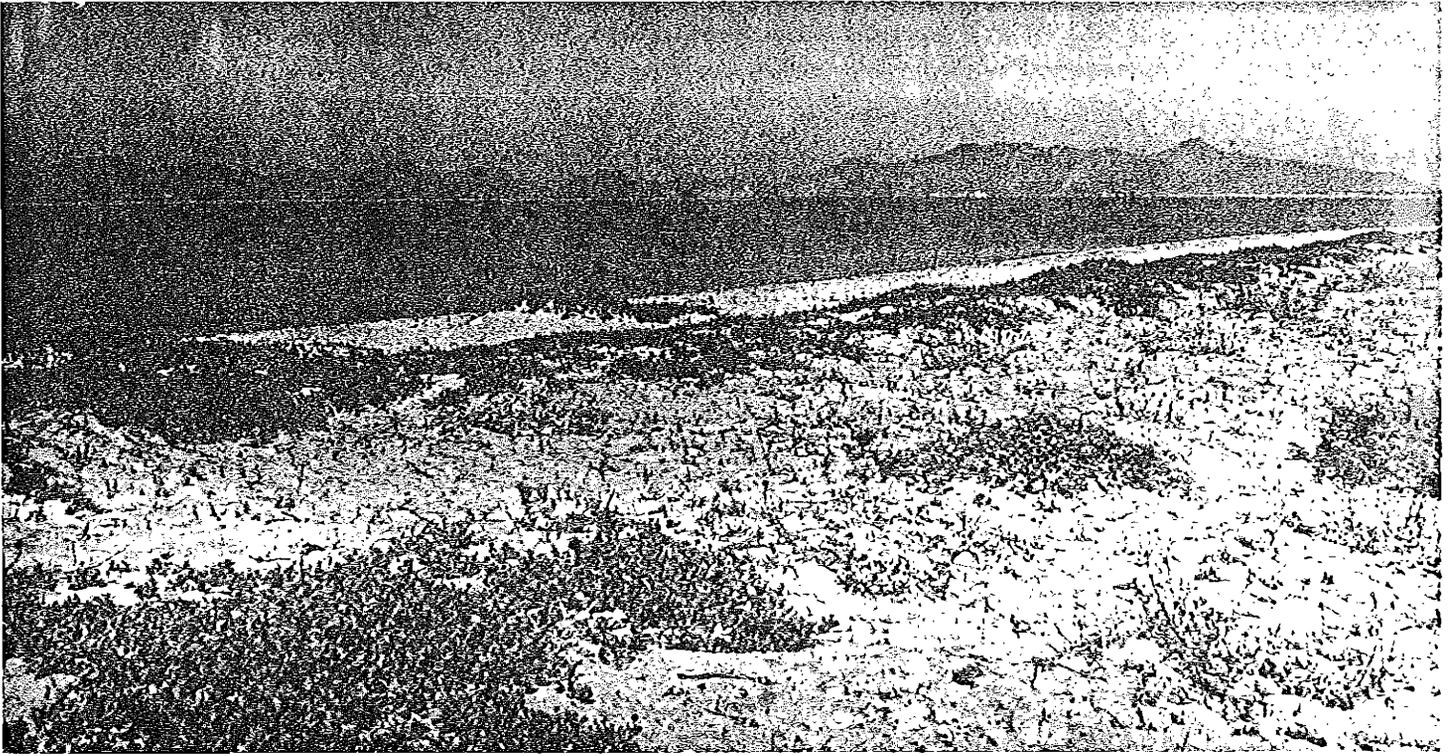


Figure 193. Sonoran maritime strand just north of Cruz Piedra, Sonora, Mexico, looking toward Empalme. An open "beach" strand of Sandverbena [*Abronia maritima*], Beach Sunflower [*Helianthus niveus*] and Pickleweed [*Salicornia* spp.].

Ángel de la Guarda and Tiburón, communities consist of relatively few species that show great seasonal population fluctuations. About 60 species of fishes occupy this zone near Puerto Peñasco, Sonora. The most abundant kind is the Panamic Sargeant Major [*Abudefduf troscheli*] followed by the Gulf Opaleye [*Girella simplicidens*], two clinid blennies [*Paraclinus sini*, *Malacoctenus gigas*], and the Sonoran Goby [*Gobisoma chiquita*]. The strand inhabiting clingfishes (e.g., *Tomicodon humeralis*, *Gobiesox pinniger*, etc.) are also common, rarely occurring below mid-tidal zones, and daily exist for a period of hours above the level of the sea. A major piscivore is the Spotted Sand Bass [*Paralabrax maculatofasciatus*]. Over the long term, warm-temperate species dominate the community in numbers and biomass—Gulf Opaleye, Spotted Sand Bass, Rock Wrasse [*Halichoeres semicinctus*], Sargo [*Anisotremus davidsoni*], and Bay Blenny [*Hypsoblenius gentilis*]. These are cold-tolerant species able to survive occasional low sea temperatures that decimate several tropical species in this region, especially Panamic Sargeant Major (Thomson and Lehner, 1976).

The central Gulf has about twice as many species as the upper portion and they are far more colorful than the drab, cryptic fishes characterizing upper-gulf shorelines. Warm-temperate species so common nearer the Colorado Delta are absent or uncommon here. The Panamic Sargeant Major remains abundant, but the Cortez Damsel fish [*Eupomacentrus rectifraenum*] becomes one of the more conspicuous forms. A dominant piscivore is the Leopard Cabrilla [*Mycteroperca rosacea*] (Hobson, 1968). Angelfishes [*Pomacanthus zonipectus* and *Holacanthus passer*] and butterfly-fishes [*Chaetodon humeralis* and *Heniochus nigrirostris*] are frequent, as are several species of wrasses [*Halichoeres nicholsi*, *H. dispilus*, *Bodianus diplotaenia*, *Thalassoma lucasanum*]. Larger prey items are taken by Baja Grouper [*Mycteroperca jordani*], while

Spotted Sand Bass is replaced by Flag Cabrilla [*Epinephelus labriformes*] as a major predator on smaller species. Moray eels [*Gymnothorax castaneus* and *Muraena lentiginosa*] become common, occupying the predatory niche at night. Bumphead Parrotfish [*Scarus perrico*] and Yellowtail Surgeonfish [*Prionurus punctatus*] are common herbivores in the system, and schools of grunts [*Microlepidotus inornatus* and *Haemulon sexfasciatum*] cruise over reefs and feed on sandy areas nearby. Further south, out of the area, species of Indo-west Pacific origins have become established, and on the peninsula side of the Gulf, the shoreline fauna is equally as rich as any in that region (Thomson et al., 1979).

Numerous other small shore fishes, related to those discussed for the California coast, also occur in profusion in the Sea of Cortez. Soft bottoms are occupied by about half the known fauna of ca. 30 species of gobies. Especially characteristic are the estuarine Guaymas Goby [*Quietula guaymasiae*] and Longtail Goby [*Gobionellus sagittula*]. Mulletts [*Mugil cephalus*, *M. curema*] feed on detrital materials associated with muds, and in shallows fall prey to nets of local fishermen. Mojarras [*Gerres cinereus*, *Diapterus peruvianus*, *Eucinostomus* spp.] also are abundant. The Longjaw Mud-sucker, shared by both Gulf and California coasts, can use atmospheric oxygen when stranded by low tides (Todd and Ebeling, 1966). And, an important counterpart of the Californian Grunion is the strand-spawning Gulf Grunion [*Leuresthes sardinalis*], the young of which migrate to soft- or sand-bottomed areas for food and shelter. Muds grade into sandy substrates, where Stingrays [*Urolophus halleri*], mojarras, mulletts, Grunts [*Pomadasyx branicki*], various croakers [*Cynoscion parvipinnis*, *Bairdiella icistius*], Bonefish [*Albula vulpes*], and some flounders [*Etropus crossotus*, *Achirus mazatlanus*, *Symphurus melanorum*, and others], hold forth (Thomson, 1973, Thomson et al., 1979).

Sonoran Interior Strands

Stream channels and other interior strands of tropic Sinaloan and sub-tropic Sonoran zones are typically occupied by open stands of scrub (e.g., *Baccharis salicifolia*), shrubs (e.g., Tree Tobacco, *Nicotiana glauca*), and weeds (Careless Weed (*Amaranthus palmeri*), Thorn Apple (*Datura* spp.), nightshade (*Solanum* spp.), sunflower (*Helianthus* spp.), and dock (*Rumex* spp.)). Wetter sites have a correspondingly greater herbaceous cover and may present a dense stand of annuals, particularly Cocklebur (*Xanthium strumarium*), Rabbit's Foot Grass (*Polypogon monspeliensis*), and diverse composites. Other less-watered basins and channels, or those subject to frequent scours, may be populated only by algae or only very early successional species. As is the case with strands everywhere, the substrate may be of mud, sand, rock, or rubble (Figs. 143, 194, 195).

Plant-animal relationships within these linear and basin communities remain largely unstudied and therefore are poorly known. Smaller desert streams often meander in aggraded, braided channels through sandy beds where change is constant (Figs. 143, 147). Over a period of a year, fluctuations in water levels are pronounced, so that aquatic and semi-aquatic animals may simply survive in periods of drought in greatly reduced, permanent segments, and fulfill their principal biological function of reproduction in winter months of higher flow or after spates produced by summer rains. The concept of strands, therefore, may be applied even to some fishes that have become adapted to such extremes, e.g., Longfin Dace and Sonoran Topminnow. The remarkable Longfin Dace has been recorded to survive partial desiccation beneath mats of algae when evaporation lowered stream levels (Minckley and Barber, 1971), and the livebearing topminnows have a similarly remarkable tenacity of life, persisting in drying pools at high temperatures and in foul conditions. Survival of a single female topminnow may insure population of an area as a single insemination may be used for consecutive broods. Numbers of embryos appear food related so that in an expanded habitat following rainfall, a female may produce many young and employ superfetation to increase her reproductive rate (Schoenherr, 1977). Growth rates of both these "desert-adapted" fishes is rapid, and reproductive individuals can appear in a few weeks.

Other stream animals (e.g., aquatic insects) have recently been demonstrated to have remarkably short life cycles, so that vagaries of the environment are circumvented by aerial life-history stages at all times of year. Death from desiccation in isolated channels or by flash flood is balanced by continuous reproduction and development from egg to adult in as few as 7 days (Gray, 1980). Perhaps, as suggested by Gray, this remarkably high turnover coupled with very high rates of production in desert streams (Busch and Fisher, 1981) aids in explaining high densities of insectivorous birds (and bats) along their courses. Expansion of research on water-land interactions in strands should provide information far out of proportion to their physical size and apparent importance in southwestern arid zones.

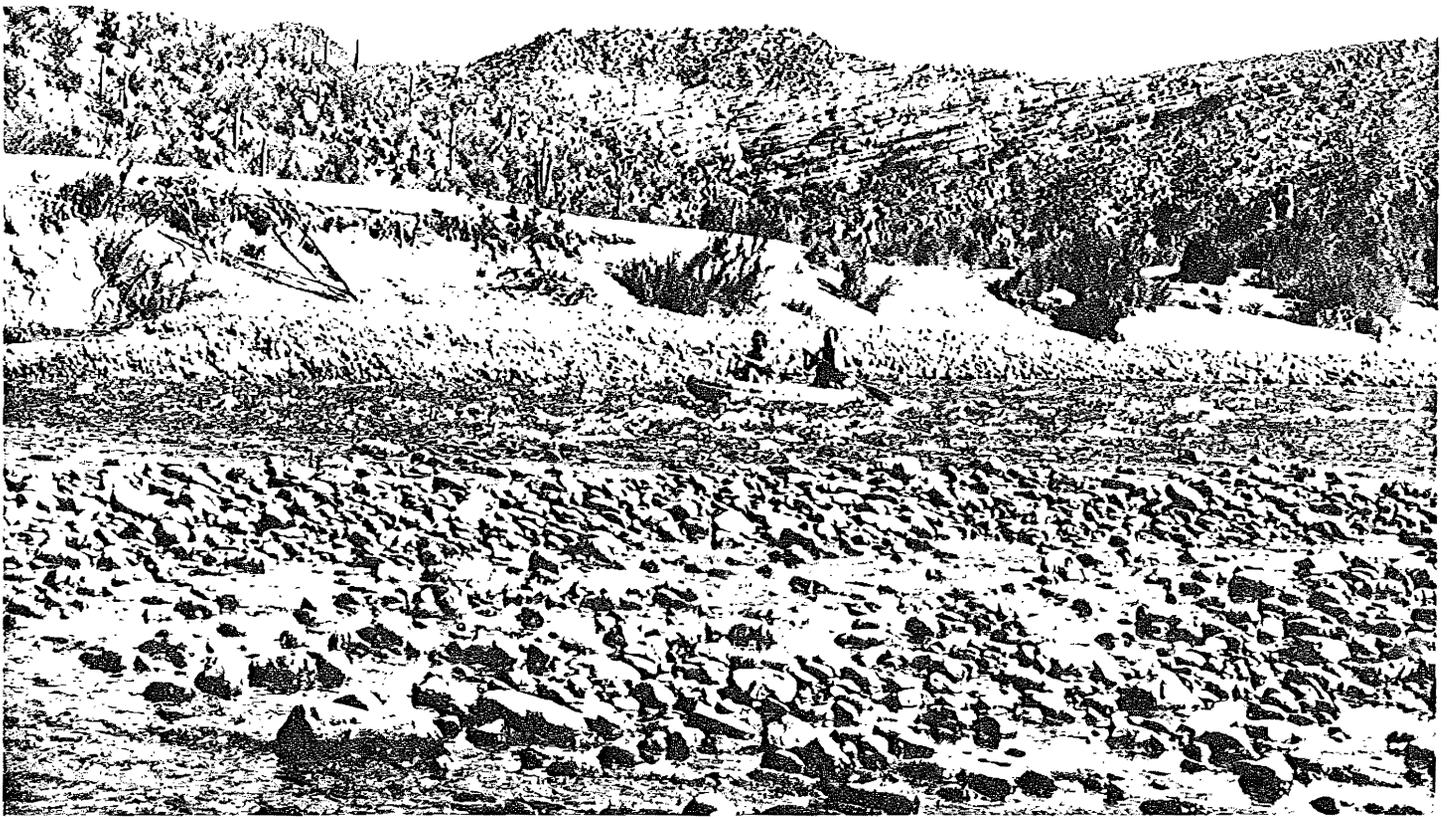


Figure 194. Riparian strand within the Sonoran Desert on the Salt River, Gila County, Arizona. Desiccated algae on rock rubble habitat occupies the more frequently inundated channel of the stream; sand substratum of the periodically flooded plain supports an open population of Saltcedar [*Tamarix chinensis*]. Elevation ca. 750 m.

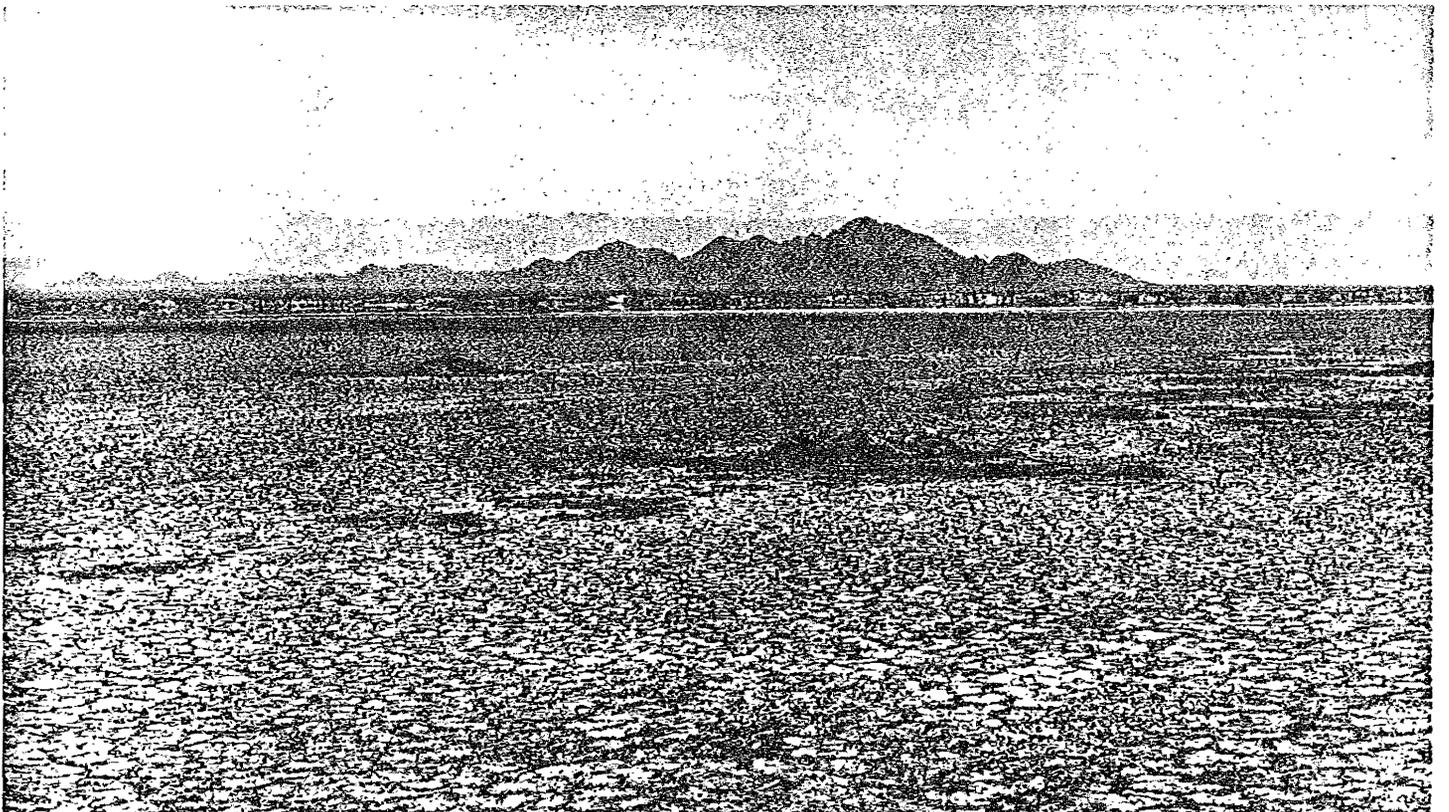


Figure 195. The almost unvegetated strand of Laguna Salada, Baja California del Norte, Mexico. Inundated infrequently, these playa habitats were nonetheless wetlands and should be considered as such. This "dry lake" is now being filled with return water from agricultural drains through the Rio Hardy—in effect a managed repetition of the Salton Sea experience in the United States. Elevation ca. -3 m.

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