CHAPTER 1

General Description of the Colorado River

INTRODUCTION

The Colorado River, which is 1,397.25 miles in length (2250 km), begins its long journey to the Gulf of California in Grand County, Colorado on the Continental Divide (Ghassemi et al., 1995). It is formed by many small streams that receive an abundance of water from melting snows high in the Rocky Mountains. These snows normally keep the river so full that a portion is siphoned off through the Continental Divide via Adam's Tunnel to the Big Thompson River. This river is the source of irrigation of the South Platte River valley in northeastern Colorado.

At the end of the canyon the swollen Colorado receives Fremont and Escalante drainage from the Great Arid Kaparowitz Plateau. The Colorado River is joined by the Gunnison, which is formed by the North and South Branches. The Uncompahgre River joins the Gunnison, which then joins the Colorado. Farther downstream the San Miguel and Dolores Rivers join the Colorado River in northern Utah.

The Green River, which is the longest tributary of the Colorado River, joins it in Utah. It receives many tributary streams (Figure 1.1). The Green River rises in the Wind River Mountains of Wyoming and is fed by a dozen creeks. From Wyoming the Green flows across the northeastern corner of Utah, receiving still more melted snow from the Uintah Mountains, the only major east–west range in the Rocky Mountain System and the highest point in Utah. Looping through northwestern Colorado, the Green is joined by the Little Snake from the Medicine Bowl Range of Wyoming and the Yampa and the White Rivers of Colorado. Curving back into Utah, the Green gathers from the west the Duchesne, Price, San Rafael, and the Dirty Devil

Figure 1.1. Map of Colorado River basin.

Rivers of Utah. Moab Canyon of Utah intersects with the Green River. The next river to join the Colorado is the Escalante River in the mouth of Lake Powell. Lake Powell is a large lake formed behind the Glen Canyon Dam.

The San Juan joins the Colorado in the area of Lake Powell and forms a long estuary in Lake Powell. Many tributary streams join the San Juan in Colorado, New Mexico, and Utah (Figure 1.1). The San Juan is not only Colorado's largest river, but the largest river in New Mexico. Its annual discharge is 2,500,000 acre-ft, which is over twice that of the noted Rio Grande. The headwaters of the San Juan are in southwestern Colorado near Wolf Creek Pass. Flowing south and west it bends through New Mexico for 100 miles (62 km), irrigating a mere 50,000 acres out of 600,000. Rivers draining into the San Juan are the Navajo River, Piedra River, Plata River, Los Piños River, Florida River, Animas River, Mancos River, Aztec Wash, McElmo Creek, and Yellowjacket Canyon, all from Colorado. From New Mexico, the rivers draining into the San Juan are the Chaco, Blanco Canyon, Gallegos Canyon, Jaralosa, Carrico, and Largo Creeks, and from Utah the Montezuma and Gypsum Creeks. The San Juan cuts its way through Utah to join the Colorado. In Arizona, approximately 200 river miles (321.87 km) south of the junction of the Colorado and the San Juan, the Colorado receives the Paria River from Bryce Canyon, Utah.

Vasey's Paradise is a spring in Marble Canyon located between river miles 31 and 32.[1] It drains the eastern part of the Kaibab Plateau. Water cascades down redwall cliffs to terraced slopes at the base of the falls. The abundant vegetation near the spring consists of dense stands of monkeyflower and poison ivy (*Rhus radicans*). Water temperature near its confluence with Colorado River varies from 9 to 18.5°C. The specific conductance ranges from 248 to 420 μS cm^{-1} and the pH is 8.4.

Buck Farm Canyon is an intermittent stream that enters the Colorado River at river mile 41. Little Nankoweap Creek is a small, intermittent stream that enters the Colorado River between river miles 51 and 52. The Little Colorado, which drains 141,155 km^2 in eastern and northern Arizona, enters the Colorado River between river miles 61 and 62. Salt cedar and coyote willow occur near the confluence, while farther upstream, stands of salt cedar and some sparse stands of the common reed (*Phragmites australis*) are found along the margins of the river. The water temperature at the confluence of the Little Colorado was 8.5 to 14.5°C during the period studied. Where the Little Colorado enters the Colorado River, the pH is 7.8 to 7.9. Unkar Creek is a small intermittent stream that enters the Colorado River between river miles 72 and 73. Near the mouth of the creek the vegetation consists of cane beard grass (*Bothriochola barbinodis*), sawgrass (*Cladium californicum*), and the common reed. Clear Creek enters the Colorado River from the north near river mile 84. The specific conductance at the mouth of the creek was 350 to 1700 μS cm^{-1}, and the pH ranged from 8.1 to 8.6. Bright Angel Creek enters the Colorado River on the north rim between river miles 87 and 88. The specific conductance at Bright Angel Creek ranges from 220 to 450 μS cm^{-1} at the mouth. A pH of 8.0 to 8.2 is quite stable at the

[1]There is some discussion about the exact location, but the mileage we have used comes from Stevens (1983).

confluence of the creek with the Colorado River. Pipe Creek enters the Colorado River from the south between river miles 88 and 89. The vegetation along the river is sparse and consists of seep willow, Bermuda grass (*Cynodon dactylon*), and scratch grass. Specific conductance ranges from 430 to 590 μS cm^{-1} at the confluence and from 480 to 600 μS cm^{-1} at the upstream site; pH is 8.0 to 8.7 at the mouth and 8.0 to 8.6 upstream. Hermit Creek enters the Colorado River from the south at river mile 95. Its source is a number of springs along the south rim.

Crystal Creek enters the river from the north rim between river miles 98 and 99. No vegetation grew at the confluence of this stream with the Colorado River. Upstream, the canyon is wide, with an open overstory of salt cedar and seep willow. The specific conductance at the mouth was 140 to 474 μS cm^{-1}. Upstream, this value ranged from 240 to 420 μS cm^{-1}. The pH was 8.0 to 8.1. Shinumo Creek enters the Colorado River from the northwest between river miles 108 and 109. White Creek joins Shinumo Creek 5 miles (8.05 km) from the mouth of Shinumo Creek. Occurring along the margins of the stream are seep willow and satintail (*Imperata brevifolia*). The water temperature of Shinumo Creek at its mouth was 8.0 to 20°C. Near the base of the waterfall the temperature varied 10.5°C. Elves Chasm is located between river miles 116 and 117, where Royal Arch Creek enters the Colorado River. Very little vegetation is present at the mouth of the creek.

A short distance upstream, just above the high-water mark of the Colorado River, are several small pools. Vegetation along the margins of these pools consists of seep willow, salt cedar, and redbud. The temperature fluctuates over the seasons and varies from 8.5 to 17.5°C. Specific conductance varies from 429 to 1200 μS cm^{-1} at the mouth and from 525 to 940 μS cm^{-1} upstream. The pH is 8.1 at the mouth.

Stone Creek enters the Colorado River from the north rim between river miles 131 and 132. It is an intermittent stream. Tapeats Creek enters the Colorado River near the north rim at river miles 133 and 134. Tapeats Creek contributes the largest discharge into the Colorado River from the north side of the Grand Canyon. Along the stream margins are the scouring rush (*Equisetum hiemale*), jointed rush (*Juncus articulatis*), cardinal monkeyflower (*Mimulus cardinalis*), and water speedwell (*Veronica aquatica*). Deer Creek enters the Colorado River from the north bank between river miles 136 and 137. Its source is a number of springs. Near the mouth of Deer Creek below the falls, vegetation consists primarily of seep willow, salt cedar, coyote willow, and scratch grass (*Muhlenbergia asperifolia*). The temperature variance is from 12 to 19°C. Specific conductance ranges from 350 to 442 μS cm^{-1} at the mouth. The pH is about 8.3 at the confluence during August and October.

Kanab Creek arises in Cane County, Utah and flows southward approximately 105 km into Arizona, where it enters the Colorado River between river miles 143 and 144. Marginal vegetation at the confluence with the Colorado River consists of a few salt cedars and seep willows. Upstream areas are bordered by salt cedar, bullrush, Arizona grape (*Vitis arizonica*), and cattails (*Typha* spp.). Kanab Creek is a sulfate stream and is low in nitrogen and phosphorus and relatively high in silica. 150 Mile Canyon, a small stream, flows intermittently into the Grand Canyon area between river miles 149 and 150. It is less than 2 miles (3.22 km) in length. Near the mouth of the creek are small pools and they are surrounded by seep willow, saw grass, bull-rush (*Fraxinus* sp.), and scratch grass. Bullrushes, scratch grass, blue-eyed grass (*Sisyrinchium demissum*), and maidenhair fern line the canyon walls above the falls of this creek.

Havasu Creek enters the Colorado River from the south side of the canyon between river miles 156 and 157. Havasu Creek is the only major tributary classified as an impure dolomitic stream. The creek carries carbonate waters dominated by calcium and magnesium and has a silicate concentration second only to that of Diamond Creek. Both nitrogen and phosphorus values are low in Havasu Creek. The temperature at the confluence ranges from 14° to 23.5°C, specific conductance from 660 to 740 μS cm^{-1}, and pH from 8.3 to 9.0.

National Canyon enters the Colorado River from the southeast between river miles 166 and 167. It is a small, intermittent stream. Lava Falls Spring is located between river miles 179 and 180 on the south side of Lava Falls Rapids. Three Springs Canyon enters the Colorado River between river miles 215 and 216. It is an intermittent creek and is relatively short. Vegetation is sparse at the confluence. Vegetation is more apparent upstream. Seep willow, salt cedar, monkeyflower, cattail, and common reed constitute most of the upstream marginal vegetation.

217 Mile Canyon enters through the canyon between river miles 217 and 218 and is a small, intermittent stream. Vegetation is limited to a few seep willows and alkali golden bush.

Diamond Creek enters the Colorado River from the north between river miles 225 and 226. Below the springs Diamond Creek is intermittent. At its mouth it is wide, with little vegetation. Seep willow, cattails, and rabbit foot grass (*Polypogon monspeliensis*) occur at or near the margins of the stream. Water temperature at the mouth ranged from 12 to 27°C. Travertine Falls is located between river miles 230 and 231 on the south side of the canyon. It is a small waterfall approximately 24 m in height and about 200 m from the Colorado River. It forms an intermittent stream. Bridge Canyon is located between river miles 235 and 236. It is a small intermittent creek. Its average gradient is 152 m km^{-1}. No vegetation was observed growing at the edges of the pools.

Above the Hoover Dam at Grand Wash (river mile 276), the river turns sharply right and flows south again, forming the boundary between Arizona and Nevada. In this area it is joined by the Virgin River from the Zion Canyon. The Colorado receives the Bill Williams River, which drains 5400 square miles in Arizona.

Near Yuma, the Colorado receives the Gila River, which rises in the Elk Mountains. It is 630 miles (1010 km) long and one of the most important rivers in America's Southwest. The Gila flows through some of the most arid and desert country in the United States. The Coolidge Dam was constructed in 1928 on the Gila River with a reservoir to hold 6000 million feet (171,428,570 m^3) of water. Arizona's largest river, the Gila drains an area of approximately 56,000 square miles (34,720 km^2), part of which is in New Mexico, where the headwaters of the river are in the Mogollon Mountains.

The Gila River on its course through Arizona receives the San Francisco River, which comes down from the northeast. The Gila alternates its course from southwest to northwest in reaches of 20 to 60 miles (32 to 96 km) through several towns before entering the Gila Indian Reservoir in Pinal County. The chief tributaries of the Gila are the Salt, the San Simon, the San Pedro, the San Carlos, the Santa Cruz, the San Francisco, the Agua Fria, and the Hassayampa Rivers. The Gila also receives numerous intermittent streams and creeks.

The Salt River is a tributary of the Gila formed by the union of the Black and White Rivers in the Mogollon and Black Mountains. Later it is fed by the Tonto Creek from the High Tonto Basin. On the Salt River is the Roosevelt Dam and Reservoir, which irrigates a large portion of southern Arizona.

Downstream from the Hoover Dam is Davis Dam, which has formed Lake Mohave and provides considerable water for irrigation and power generation. The Hoover Dam, on the Colorado River, is mainly for power generation, but also performs other functions.

The Colorado River then flows generally in the southerly direction, forming the borders between California and Arizona. The next humanmade impediment is Parker Dam at the southeastern end of Lake Havasu. The Parker Dam is the beginning of the Colorado Aqueduct, which carries water 389 km across the Mojave Desert and mountains to the city of Los Angeles and other areas of southern California. The two other large reservoirs on the Colorado River are the Imperial and the Laguna Reservoirs. These two reservoirs furnish a large amount of water for irrigation in the desert.

For 80 miles (49.6 km) the Colorado flows through Mexico, separating areas known as Sonora and the mainland from the upper district of the penninsula of lower California. Winding through a maze of salty marshes, deserts, geisers, and dry lakes, it splits into a main channel and tributaries. The river moves slowly into the Gulf of California and sinks its red waters into the blue waters of the ocean.

REGIONS OF THE COLORADO RIVER

The flow of the Colorado River is highly variable. Historical records indicate that it has varied from less than 6 million to more than 20 million acre-feet per year. To meet downstream demands during dry periods, a system of reservoirs has been created which allows sufficient storage water to maintain the flows of the river during these periods. Besides the major reservoirs, there are numerous small reservoirs on the tributaries of the Colorado River (Figure 1.1). These reservoirs now have a combined storage capacity equal to approximately four times the total average annual virgin flow of the Colorado River.

The Colorado Basin has three distinct regions covering 244,000 m^2 or 156,160,000 acres (Brown, 1927).

Upper Basin. The Upper Basin lies in Colorado, New Mexico, Utah, and Wyoming between the Wasatch and Rocky Mountains. This region receives heavy precipitation in the form of snow and provides 75% of the river's flow. In this area the rainfall is less than 10 in. (25.4 cm)/yr over the valleys of the Upper Basin, but irrigation in the valleys has been adapted to agriculture and manufacturing (Brown, 1927).

Plateau Section. The plateau section from Lees Ferry to Grandwash Cliffs has an elevation of 2000 to 8000 ft (609.6 to 2,438.4 m) and is cut by deep gorges and canyons (Brown, 1927). This plateau section contains the area known as the Grand Canyon.

Lower Basin. The Lower Basin lies in Arizona, California, Nevada, and Mexico only a few feet above sea level. It has a precipitation rate of 1.5 to 8 in./yr, with temperatures ranging from 32 to 120°F. A temperature of 130°F has been recorded in the Salton Basin. This basin is separated from the Colorado by a deltic ridge and by the river itself. The basin is below sea level and 100 ft below the Colorado River (Brown, 1927).

The dominant characteristics of the Colorado are its profile, which through much of its course has little slope and is slow moving, and its large silt load. In its 1397-mile (2248.25 km) length, the river falls 8000 ft (2438.4 m). If one eliminates the steep slopes of the headwaters of the Green River, there is a drop of 4000 ft. For half this distance the river flows in a canyon. The Yuma River carries approximately 100,000 acre-ft of silt annually into the Colorado.

DAMS

A large number of dams have been built on the Colorado River system (Figure 1.1). Many of these are on tributaries and are relatively small. These dams were built to supply water used to irrigate farmland. Other dams are placed in deep gorges, where the fall of the water is great. These are rather expensive dams to build but pay for themselves because of the electric power they generate. One of the largest dams is the Hoover Dam, which was authorized in 1928 and finished in 1930. The Cooley Dam, on a tributary of the Gila River, was authorized in 1931 and construction was started in 1933. It was finally finished in the late 1940s. The Flaming Gorge Dam was built on the Green River and the Black Canyon Dam on the Gunnison River. The Red Canyon Dam was built near the Hoover Dam. The Dolores Dam was built on the Animas River, the Yampa Dam on the San Miguel River. As stated above, these dams were constructed primarily for agricultural use or for the generation of power and the supplying of water. The larger dams were built to supply water to the various Compact states (Committee to Review the Glen Canyon Environmental Studies, 1991).

On the main stem of the Colorado River is the Glen Canyon Dam, which is at the head of the reach of the river commonly known as the Grand Canyon. The large lake that it forms is Lake Powell. This lake is approximately 80 miles (128.75 km) long. The Green River enters the Colorado River at the head of Cataract Canyon. The land along the upper Green River is heavily irrigated, as is the land beside the two major tributaries, the Yampa and White Rivers. Other tributaries entering Lake Powell below the Glen Canyon Dam are the Little Colorado River and Kanab Creek.

Lake Mead is a large lake formed by the Hoover Dam. Lake Mojave and Lake Havasu are smaller lakes along the Colorado River.

Besides the Glen Canyon Dam and the Hoover Dam, other dams on the lower Colorado River are the Headgate Rock Dam, the Palo Verde Diversion Dam, the Imperial Dam, and the Morelos Dam in Mexico.

GEOLOGY OF THE WATERSHED

The geology of the Colorado River basin is highly varied. It is composed of igneous, metamorphic, and sedimentary rock types. They range in age from 500 million years to recent alluvial deposits. Structurally, the geology adds anticlines, domes, and faults to the topographic relief and the geohydrology of the region. Sedimentary formations found in the basin were deposited in marine or brackish-water environments. Bedded and disseminated sodium chlorides (halite) and calcium sulfate (gypsum) found as clays have high contents of exchangeable sodium and magnesium (U.S. Department of the Interior, 1997).

Soils

As one might expect, the soils of the basin resemble the geologic formations from which they were derived. The residual soils were derived from shale or sandstone and are generally shallow. These soils contain appreciable soluble mineral content, due to residual and secondary mineral formation from parent material. Upon weathering or irrigation, salts may accumulate on or near the surface, due to evaporation or consumptive use by plants (U.S. Department of the Interior, 1997).

Geology

Sedimentary formations that were deposited in marine or brackish-water environments are found in the basin. Bedded and disseminated sodium chloride (halite) and calcium sulfate (gypsum) are found as clays with high contents of exchangeable sodium and magnesium. The Grand Canyon's older Precambrian rocks are made up of the Vishnu Group, the Zoroaster Plutonic Complex, and the Trinity and Elves Chasm Gneisses. The Vishnu Group is composed of highly metamorphosed schists and gneisses that were originally sediments and minor mafic igneous rocks. These rocks were completely deformed by metamorphism. In the Lower Basin they are imprinted with a well-developed subvertical schistosity (Brown and Babcock, 1974).

Protruding on the Vishnu Group probably during and after regional metamorphism were granite plutons of the Zoroaster Complex. The last episode of activity, probably a hydrothermal rather than a magnetic event, produced pegmatite and aplite dikes and sills. The Trinity and Elves Chasm Gneisses contain layers of the Vishnu formation that grade at their boundaries into the Vishnu Group. These formations demonstrate a metasedimentary origin for these rocks. However, over large areas the gneisses are homogeneous and quartz–monzonite to quartz–dorite in composition. The origin of these formations is unknown; however, their structure gives them an affinity to igneous rocks (Brown and Babcock, 1974).

Zones of intense shearing developed after metamorphism and plutonism. Movement offset metamorphic grades as much as several kilometers vertically in some zones and also caused local retrogressive metamorphism (Brown and Babcock, 1974).

In the reach of the river through Marble and Grand Canyons, the Colorado River cuts along a number of distinct geologic strata, ranging in age from 180 million years (Jurassic) to 1.5 billion years (Precambrian). In Marble Canyon, from Lees Ferry to approximately river mile 51, the Colorado River cuts through late Paleozoic and Metazoic formations, the majority of which are highly resistant to erosion.[2] In this section the steep walls of redwall limestone form a narrow canyon. Between approximately river miles 51 and 75, the canyon widens so that the river cuts through less resistant early Paleozoic and late Permian strata. Generally, this area is composed of mauve limestone and bright angel shale.

Between approximately river miles 75 and 240, the canyon is separated into five natural subdivisions: an upper, a middle, and a lower granite gorge, and two intervening sections where early Paleozoic rock forms vertical cliffs at river level. The upper gorge is approximately 45 km long and extends from river miles 75 to 108. This area is characterized by steep walls of highly resistant Precambrian granites and schists and a narrow (80 m), swiftly moving channel. The Precambrian rock disappears near river mile 116. The middle granite gorge begins at approximately river mile 125. Its walls are less prominent than those of the upper gorge and have only a limited thickness exposed at river level. The canyon again narrows near river mile 140, due to the Precambrian rock at river level being replaced by early Paleozoic strata. The river in this area is similar to Marble Canyon. The lower granite gorge begins at approximately river mile 215 and extends downstream to river mile 240. A relatively large portion of the lower gorge's Precambrian rock is exposed at river level. It forms a V-shaped canyon similar to that in the upper gorge (Hamblin and Rigby, 1968).

BIOLOGY OF THE WATERSHED

The flora and fauna of the Colorado River in the riparian areas is best known in that reach, commonly known as the Grand Canyon, that lies between Glen Canyon Dam and Hoover Dam. The flooding of the riparian area is much less severe than before the dams were built. The woody species of the riparian area are the component vegetation of the landscape and contribute greatly to the support of insects and invertebrates because these areas are less subject to violent floods and droughts; that is, they are more stabilized than before the dams were built (Committee to Review the Glen Canyon Environmental Studies, 1990).

Plants

Native species are a minor component of the overall flora. There are many introduced species in this area. There is an increasing predominance of salt cedar, an increasing abundance of camel thorn (*Alhagicamelorum*), and herbaceous species such as yellow sweet clover (*Melilotus officinalis*) and spiny sow thistle (*Sonchus asper*). Exotics are common along the river. In undisturbed areas they compete poorly with native plants but invade rapidly and increase aggressively when habitat disturbance removes or weakens the native vegetation. Such species are the tamarisk (commonly known as

[2] There is some discussion about the exact location, but the mileage we have used comes from Stevens (1983).

salt cedar). In much of the Southwest, salt cedar has out competed native riparian species, especially in disturbed habitats (i.e., those associated with dammed streams). However, it does not seem to have caused the loss of plant species in the Grand Canyon. Salt cedar is usually considered a poor habitat for most wildlife except mourning and white-wing doves (*Zenaida macroura* and *Z. asiatica*). As a species, it attracts insects as well as riparian birds. It is important as a shelter for recreational uses (Committee to Review the Glen Canyon Environmental Studies, 1991).

Another plant of import is camel thorn, a spiny leguminous half-shrub that has invaded several beaches, especially in the upper portions of the canyon, making them virtually unusable for camping. The Russian olive, a small tree spreading into the canyon from other sources, originated from oriental planting. This species has been planted to enhance wildlife. Mourning dove densities in Russian olive habitats were the highest reported for the northern Rio Grande Valley in New Mexico and Texas. Another woody species native to the area is the western honey mosquite, a small tree or subtree occurring in alluvial deposits. This species is important to several riparian birds. Catclaw acacia is a subtree codominant with mosquite; the coyote or sandbar willow is codominant with salt cedar. Next to the Goodding willow, brevy willow is the species preferred by beaver. The Goodding willow, which occurs only at scattered localities along the river, along with Fremont cottonwood, is at least partially prevented from spreading by beavers. Arrow weed is another clonally spreading medium-sized shrub. Seep willow, a large shrub, has two species: *Baccharis saliscifolia* and *B. emoryii*. *Baccharis saliscifolia* is more common along the river and *B. emoryii* along sidestreams. True willow, desert broom, and other medium-sized *Baccharis* occur in the lower canyon. Waterweed (a *Baccharis*), morphologically and ecologically similar to desert broom, is common. Apache plume is a dominant evergreen shrub. This species is relatively common downstream to about km 93.3. Many of the stands of this species are in poor condition, presumably from the lack of water since construction of the Glen Canyon Dam (Committee to Review the Glen Canyon Environmental Studies, 1991).

The herbaceous riparian species that are common native grasses include foxtail broom and Bermuda grass. Many herbaceous plants have been discovered in this reach of the Colorado River. A checklist in 1932 listed approximately 450 species. A second list included 650 species, and a third checklist, 900 species. Most recently, 1400 species of herbaceous plants have been recorded from this general area. Two species new to science were recorded from this area: *Euphorbia aaron-rossii* and *Flaveria mcdougallii* from Cove Canyon, a tributary of the Colorado (Committee to Review the Glen Canyon Environmental Studies, 1991).

Amphibia

In 1970, numerous species of plants and animals were added to the Grand Canyon checklist. Previously, Tomko (1975) added nine species to Gehlbach's 1966 checklist. Amphibians in general are associated with moist habitats. Found were one species of salamander and five species of toads and frogs, four of which were associated with the Colorado River. Woodhouse's toad (*Bufo woodhouseii*) is restricted to the Colorado corridor, and the leopard frog (*Rana* cf. *pipiens*) is restricted to Cardenas Marsh, a postdam marsh and upper lake (Committee to Review the Glen Canyon Environmental Studies, 1991).

Reptiles

The Grand Canyon rattlesnake or pink rattlesnake (*Curtalus varidus abyssus*) occurs frequently in riparian habitats. Seven species of lizards for the riparian zone were listed by Warren and Schwalbe (1985). The stabilized river flow probably resulted in an increase in reptile populations through greater vegetation biomass, providing, in turn, more cover and an increase in insects available (Committee to Review the Glen Canyon Environmental Studies, 1991).

Birds

In the 1970s, Carothers and Johnson (1975) published a new distribution record for 20 birds in the Grand Canyon region, seven of them additions to the fauna list compiled previously. By 1978, the number of species known from the Grand Canyon region had grown to 284, adding more than 100 additional species to the 180 in the first Grand Canyon checklist of Grater (1937). By 1987 this had increased to 303 avian species (Brown et al., 1987), of which 250 or 83% had been recorded from the Colorado River corridor. Populations of nesting birds in the tamarisk approach the highest numbers in temperate North America. Proliferation of the vegetation in the postdam riparian ecosystem is largely responsible for the increase in number of species of birds, the reason being that the birds selected tamarisk over native species. Why this occurs is not clear. Most of the species recorded are insectivorous, and therefore the relatively high insect populations and low human population probably account for their being present. Of the 78 species present reported by Hoffmeister (1971), 40 occurred in the inner gorge, and most of these occurred in the riparian zone restricted to riparian mammals such as beavers, or some lesser category of usage, such as by desert bighorn sheep (Committee to Review the Glen Canyon Environmental Studies, 1991).

Two endangered bird species of the riparian zone are the bald eagle (*Haliaeetas leucocephalus*) and the peregrine falcon (*Falco peregrinus*). Bald eagles have become regular winter visitors since the mid-1980s in the vicinity of Nankoweap Creek, where they feed on fish. The Grand Canyon supports the highest concentration of breeding peregrines in the lower 48 states. A total of 71 different peregrine breeding areas were documented during partial investigation of the region in 1988–1989. A large proportion of their diet consists of riparian birds caught over the riparian and aquatic zones of the inner canyon. This riparian zone, which is rich in species in the Grand Canyon area, supports the food for fish and birds. The riparian area of the Grand Canyon is a very diversified area, and it has become increasingly moist, contrasting with the increasingly xeric conditions of most riverine ecosystems of the Southwest. Thus "riparian vegetation in the canyon is uniquely valuable since the Colorado River in Grand Canyon is the only major riverine system in the Southwest where there has been appreciable increase rather than decrease in riparian vegetation and associated animal populations" (Committee to Review the Glen Canyon Environmental Studies, 1991).

However, it should be pointed out that that the bald eagle (*Haliaeetus leucocephalus*), does not seem to be correlated with prey abundance, biomass patterns, or habitat conditions associated with eagle foraging. Rather, it seems that human activity may in some cases be responsible for lower eagle abundance in some reaches of the river.

However, it should be pointed out that the dam-related effects of clarity, pattern of flow, and water temperature did not override the geomorphological influences on habitat availability. The recovery of the benthos did not seem to be correlated with the abundance of fish but rather with the geomorphological differences in substrate availability between reaches, mediated by the dam and tributary effects on water clarity and the amount of benthos. The action between flow regulation and geomorphology produced a pattern of circuitous recovery of some physical river ecosystems, usually characterized by distance from the dam. This was not true for the benthos. Improving discharge management for endangered native fish population requires detailed understanding of the existing and potential benthic development and trophic interactions. It has been said that many factors are involved in the recovery of the benthos and hence the fish population (Stevens et al., 1997).

Mammals

The vegetation is very important as food and shelter to mammals. In some situations mammals have a profound influence on the vegetation. For example, herbivorous mammals caused severe damage to vegetation by trampling and reducing populations of some plant species by selective foraging prior to the removal of these feral animals from the canyon. For example, the lack of establishment of Goodding willows and Fremont cottonwoods was probably due to beavers. Beavers also eat the smaller coyote willow and even tamarisk. Foraging of beavers could produce a beaver disclimax of some beaches if the beaver population was large enough. One of the most poorly understood vegetational parameters for most woody riparian species is seedling establishment. For such a large and diverse area, Glen Canyon is notably short on endemic, rare species. Two such species are previously undescribed species of flowering plants, *Flaveria mcdougalii* and *Euphorbia aaron-rossii*.

It is very evident that the riparian areas of the Grand Canyon reach of the Colorado River are very important for the aquatic life of the river, and vice versa. Thus, the high diversity of aquatic life helps to support the high diversity of life in the riparian area, particularly birds and amphibia, and vice versa. The aquatic insects of this area are very important to the fish (Committee to Review the Glen Canyon Environmental Studies, 1991).

RIVERINE STRUCTURE

Areas where armoring has not reached equilibrium are more common in the stretch between the Little Colorado and Lake Mead than between the Glen Canyon Dam and the Little Colorado since the lower river has a much larger sediment input. Between Lees Ferry and Separation Rapids, the Colorado exhibits a typical pool-rapid morphology, with the river dropping approximately 677 m over the 384-km distance.

Rapids are constrictions in the river channel caused by the deposition of debris which are typically areas of accelerated flow and high gradient. Often, the velocities are between 3 and 5 m s^{-1} and the gradient is from 0.5 to 2 m per 100 m in the rapids. Fifty percent of the 677-m elevation change occurs in the 161 rapids (Dolan et al., 1978; Leopold, 1969). Separating the sequences of rapids are areas of greater width, slower velocity, and shallower gradients. The velocities in these areas are from 0.3 to 0.6 m s^{-1} and the gradient is 0.5 m per 100 m (Leopold, 1969).

The discharge of the river varies with width and depth. Under the present flow regime the average width is about 200 m, with a range from 80 to 320 m. The average depth of the river is about 10 to 12 m, although the longitudinal profile is highly irregular. The majority of the deeper pools occur immediately below major rapids, where the water flow emerges as a jet directed toward the riverbed. The scouring of the riverbed forms the pools. The deepest pool measured was 35 m. Usually, the shallow portions of the river occur upstream of the rapids, where the river channel is wider.

At the constriction of the river channel, which occurs in the vicinity of rapids and riffles, the larger portion of the downstream flow is directed against one bank, resulting in a strong upstream surge against the opposite bank. At times these backwaters or eddies may occupy 80% of the total width of the river. Often, sediment deposition and erosion take place in these eddies since they typically have a lower velocity than that of the general river.

CHEMISTRY OF THE WATER

The chemistry of Colorado River water is derived from graphs of the characteristics of the water between river mile 0 and river mile 240 from Lees Ferry (Table 1.1). These results clearly indicate that Colorado River water is of medium hardness, containing many trace metals, which are no doubt derived from the geology of the substrate through which the river passes. Chemical data for the water could not be located that were as thorough as those given in these charts, which we have interpreted from tables of Sommerfeld et al. (1976) (Table 1.2).

During the period when the river was studied by Carothers and Minckley (1981a), the temperature ranged between 6 and 15°C. Usually, temperatures increase downstream during the summer months. During 1975 and 1976 the temperatures varied between 7 and 17.2°C. This was in contrast to predam conditions, when the temperature ranged from 0 to 29.5°C. The specific conductance corrected to 25°C varied from 830 to 16,000 μS cm^{-1} in 1977 and 1978. By contrast, predam conductances varied between 318 and 2430 μS cm^{-1} at Lees Ferry, up to 2900 μS cm^{-1} in stretches down river of the Little Colorado. The pH varied between 7.1 and 7.9 during the study period. The major ions in the main stream were $SO_4 > CO_3 >$ chlorides. There was little change in the amounts of these ions between Lees Ferry and Diamond Creek. The ranking major cations were sodium > calcium > magnesium > potassium (Cole and Kubly, 1976).

3356 P-01 2/10/00 12:34 PM Page 14

TABLE 1.1. *Sites Sampled Along the Colorado River in the Grand Canyon National Park and Vicinity*

Site	River Mile
1. Paria River (Lees Ferry)	0.5
2. Vasey's Paradise	31.9
3. Red Wall Cavern	33.0
4. Showerstall Seep	35.5
5. Nautiloid Seep	36.0
6. Buck Farm	41.0
7. Little Nankoweap Creek	51.5
8. Little Colorado River	61.5
9. Cardenas Creek	71.0
10. Unkar Creek	73.0
11. Clear Creek	84.0
12. Bright Angel Creek	87.9
13. Crystal Creek	98.5
14. Shinumo Creek	108.9
15. Elves Chasm	116.5
16. Fossil Rapids	125.0
17. Stone Creek	131.0
18. Tapeats Creek	133.5
19. Deer Creek	136.3
20. Kanab Creek	143.5
21. Olo Creek	145.5
22. The Ledges	152.0
23. Havasu Creek	156.9
24. Prospect Lake	179.0
25. Pumpkin Springs	212.0
26. Three Springs Canyon	215.5
27. Diamond Creek	226.0
28. Travertine Canyon	229.2

Source: After Stevens (1983).

TABLE 1.2. *Chemical Characteristics of Colorado River Water 0 to 240 Miles from Lees Ferry*

	Miles from Lee's Ferry					
	0–40	40–80	80–120	120–160	160–200	200–240
Calcium (ppm)						
June	50.4, 48	49.6, 47.1, 50.4	51.2, 50.4, 52, 50.4	51.2, 48, 49.6	48	49.6
August	46.4, 47.1	46.4	57.6			67.2
Magnesium (ppm)						
June	25.4, 26.2, 24.2	25.7, 24.6, 26.5	27.3, 26.2 27.3, 26.2	26.5, 25.8, 26.5	27.6	26.5
August	23.5, 233.8	23.1	26.5			28.8
Potassium (ppm)						
June	3.44, 3.40, 3.40	3.44, 3.76, 3.48	3.68, 3.68, 3.68, 3.56	3.56, 3.56, 3.56	3.68	3.68
August	4.48, 3.36	3.36	4.28			4.92
Sodium (ppm)						
June	68.8, 68.8, 63.2	68, 65.6, 73.6	75.2, 76, 77.6, 73.6	74.4, 78.4, 81.6	81.6	74.4
August	65.6, 64	64.8	81.6			84.8
Cadmium (ppb)						
June	0.31, 0.38, 0.15	0.15, 0.15, 0.15	0.15, 0.15, 0.15, 0.15	0.15, 0.15, 0.38	0.15	0.46
August	0.38, 0.92	0.31	0.46			0.54
Cobalt (ppb)						
June	1.9, 0.77, 2.7	0.4, 2.7, 0.4	1.9, 0.77, 1.5, 1.2	0.77, 3.8, 6.5	0.77	2.7
August	1.2, 0.77	1.2	8.8			1.9
Chromium (ppb)						
June	6.5, 6.9, 1.5	4.6, 8.5, 5.8	5.4, 6.9, 5, 4.6	6.2, 5.4, 5.8	5	4.6
August	4.2, 5	5.8	8			1.2

(continues)

TABLE 1.2. *Continued*

	Miles from Lee's Ferry					
	0–40	40–80	80–120	120–160	160–200	200–240
Copper (ppb)						
June	8, 4.2, 5.8	3.5, 4.6, 5	4.6, 4.6, 4.2, 4.2	6.5, 5, 5	6.2	4.2
August	5.4, 5.8	8.8	12.3			19.2
Iron (ppb)						
June	160, 160, 200	240, 240, 240	160, 360	120		200
August	80, 40	80	3800			4720
Manganese (ppb)						
June	4.4, 3.6, 4	5.6, 6, 8.8	15.6, 15.6, 10, 0.8	10.8, 8.4, 10.8	8.4	15.6
August	10.4, 10.4	8.8	192			288
Molybdenum (ppb)						
June	7.7, 8.1	8.8	7.3	20.4		5
August	6.5, 6.9	15.4	12.3			19.2
Lead (ppb)						
June	6.2, 5.4, 5.4	1.9, 4.2, 2.7	2.7, 3.1, 2.3, 3.8	1.9, 5, 1.9	4.6	2.3
August	8.1, 4.6	15.4	12.3			19.2
Zinc (ppb)						
June	127, 77	50	38, 50	31		12
August	31, 65	42	31			31

Source: After Sommerfeld et al. (1976).

SEDIMENT LOAD

The suspended solids carried by the Colorado River vary greatly in different sections of the river. They are also variable with different flows. In 1929, Howard estimated that the amount of suspended material carried by the Colorado River as discharged sediments from 1909–1912 and 1912–1916 was approximately 1 million acre-feet for each of the two periods. It is evident that the amount of suspended material varies greatly in different parts of the river. It also varies as much as 25 to 50% at various times of the year. The average quantity of suspended matter in surface samples was about 60% of the quantity of the bottom samples. The amount of suspended sediments is highly variable. Generally, the suspended matter increases with discharge, and the first part of the increased discharge carries the largest amount of silt.

The amount of suspended material varies in different parts of the river. In the period 1925–1927, the suspended load carried past the Grand Canyon was greater than that carried past Topock, Arizona. Both the Grand Canyon and Topock had greater loads than Yuma in 1926–1928. It should be pointed out that the samples collected at Yuma contained matter brought in by the Gila River. The Bureau of Reclamation's yearly measurements for suspended loads past Yuma for 1912–1921 averaged 178 million tons. The suspended load was not exceptionally high at Yuma for 1925–1928.

It was very difficult to make an estimate of the bedload in these areas. In making the measurements of the movement of solids, a movement in the riverbed was observed. Topock and Yuma had considerably greater movement than the sediments in the Grand Canyon. It was apparent that the quantity of material moved during a change in level of a river is large, but how much material is moved as suspended load and how much is moved as bedload is not known (Howard, 1929).

Estimates of the suspended material range from 88,000 to 250,000 acre-ft/yr. The weight per unit volume differed at different parts of the reservoir because larger, heavier particles will settle out at the head of the reservoir. It was evident that the amount of suspended material at different stations varied widely.

The sediment load has been drastically reduced in the river between the dam and the Little Colorado River. This part of the river is now clear throughout most of the year. The median sediment load at Lees Ferry has been reduced by a factor of about 200, from 1500 ppm to 7 ppm. The reduction in the sediment load is less apparent downstream because of sediment inputs from tributaries and the erosion of predam fluvial terraces. At Phantom's Reach the sediment load had been reduced by only a factor of 3.5. Currently, the Little Colorado River contributes the majority of the sediment to the Colorado River between Lees Ferry and Lake Mead. This marked alteration in patterns of seasonal flow has changed the alluvial morphology of the river. The river has eroded predam terraced deposits at many locations because large gravel and rubble have been exposed that cannot be dislodged. Erosion no longer occurs. This process, referred to as *armoring,* is especially prevalent between the dam and Lees Ferry.

ASSOCIATIONS OF AQUATIC ORGANISMS: GLEN CANYON DAM TO HOOVER DAM

The associations of aquatic organisms are best known between Glen Canyon Dam and the beginning of Lake Mead. Suspended solids carried by the flow of the river vary greatly between winter and summer. During torrential winter floods of tributaries, it might be greater than 2832 $m^3\ s^{-1}$, whereas during the summer months at low flows it was only 113 $m^3\ s^{-1}$ of sediments. The average suspended sediment load in the lower Colorado before impoundment was approximately 3.5 times greater than after construction of the Glen Canyon Dam.

Algae

The algae found in the Grand Canyon reach of the river were either attached or free-floating. Many of the free-floating forms seemed to be part of attached vegetation that had been broken off by the flow. The areas of algae attachment were some of the scoured rock faces in areas of rapids and cataracts and fine sediments in backwater, usually along the inner side of river bends. Various submerged macrophytes served as the surface for attachment of many algae. Dominant diatoms were *Diatoma vulgare* (Bory), *Gomphonema olivaceum* (Lyngb Kütz), *Navicula viridula* (Kütz), *Synedra ulna*, *Nitzschia* (Ehr), and two species of *Surirella*. They were collected in the Colorado River in the stretch between the two dams (Blinn and Cole, 1991) (Table 1.3).

Crayton and Sommerfeld (1978) reported 127 species of phytoplankton in the Colorado River. Many of these they believed to be detached species dislodged during widely fluctuating river levels. Phytoplankton (about 58%) were composed of diatoms, of which the dominant species were *Diatoma vulgare*, *Rhoicosphenia curvata* (Kütz) Grun, and *Cocconeis pediculus* (Ehr). Many of these originated from Lake Powell. For example, of the 20 dominant algal species listed for Warm Creek Bay in Lake Powell, eight species were found to be common to both the river and the lake. The cell densities of diatom species in the Colorado River after impoundment were much lower than the cell densities prior to the impoundment of the river (Blinn and Cole, 1991).

Of the algae, *Cladophora glomerata* (L.) Kütz was the dominant attached filamentous green algae in the canyon, especially between Glen Canyon Dam and the Paria River and at the mouths of tributaries. The free-flowing Colorado River during high flows also carried a lot of sestonic stream drift, including algae. Usher and Blinn (1990) estimated that *Cladophora glomerata* was the dominant alga for sites at and above Lees Ferry: 144 g m^{-2}, compared with 17.2 g m^{-2} at the mouth of various tributaries below Lees Ferry. The relatively high amount of biomass of *Cladophora glomerata* in the upstream tailwater sites may be a result of stable rock faces for attachment and nutrient-enriched waters. At Lees Ferry there were often abrupt drops in population size of *Cladophora glomerata*, which were probably due to episodes of desiccation and reduced input of nutrients. *Cladophora* thrives under continuously submerged clear-water habitats (Shaver et al., 1997). *Cladophora* growths present on the downstream side of rocks were often absent on the upstream side of

(text continues on page 37)

TABLE 1.3. *Species List: Grand Canyon National Park and Vicinity*

	Substrate[b]				
Taxon[a]	V	M,S	G,R	Source[c]	Feeding Habits[d]
SUPERKINGDOM PROKARYOTAE					
KINGDOM MONERA					
Division Cyanophycota					
Class Cyanophyceae					
Order Chamaesiphonales					
Family Chamaesiphonaceae					
Chamaesiphon incrustans, 1–27				CS	
Chamaesiphon sp.				CBT	
Order Chroococales					
Family Chroococaceae					
Aphanocapsa musicola		×		CBT	
Aphanocapsa sp.		×		CBT	
Chroococcus minor				CBT	
C. minutus				CBT	
C. turgidus				CBT	
Chroococcus sp., 1–27				CS	
Gleocapsa polydermatica				CBT	
Gleothece sp.		×		CBT	
Merismopedia glauca			×	CBT	
M. punctata			×	CBT	
Order Nostocales					
Family Microchaetaceae					
Microchaete elongata				CBT	
Family Nostocaceae					
Anabaena oscillariodes		×		CBT	
Anabaena spp.		×		CBT	
Nodularia spumigena, 1–27				CS	
Nostoc hatei	×	×		CBT	
N. paludosum	×	×		CBT	
N. punctiforme	×	×		CBT	
N. verrucosum	×	×		CBT	
Nostoc spp.	×	×		CBT	
Family Oscillatoriaceae					
Gleotrichia intermedia	×			CBT	
Katagnymene pelagica (= *Microcoleus lyngbyaceus*)				CBT	
Lyngbya aerugineo-caerulea			×	CBT	
L. aestaurii			×	CBT	
L. allegori			×	CBT	
L. cryptovaginata			×	CBT	
L. digueti			×	CBT	
L. epiphytica			×	CBT	
L. hieronymusii			×	CBT	
L. limnetica			×	CBT	
L. major			×	CBT	
L. martensiana			×	CBT	
L. mesotrichia			×	CBT	
L. nordgardhii			×	CBT	
L. perelegans			×	CBT	
L. statina			×	CBT	
L. versicolor			×	CBT	
Lyngbya spp.			×	CBT	
Oscillatoria acuminata		×	×	CBT	

(continues)

TABLE 1.3. *Continued*

	Substrate[b]				
Taxon[a]	V	M,S	G,R	Source[c]	Feeding Habits[d]
O. agardhii		×	×	CBT	
O. amoena		×	×	CBT	
O. amphibia		×	×	CBT	
O. amphigranulata		×	×	CBT	
O. angustissima		×	×	CBT	
O. articulata, 1–27		×	×	CS	
O. chalybea		×	×	CBT	
O. claricentrosa		×	×	CBT	
O. cortiana		×	×	CBT	
O. foreaiu		×	×	CBT	
O. fremyii		×	×	CBT	
O. hamelii		×	×	CBT	
O. jasorvensis		×	×	CBT	
O. lemmermannii		×	×	CBT	
O. limnetica		×	×	CBT	
O. limosa, 1–27		×	×	CS	
O. migro-viridis		×	×	CBT	
O. mougeotii		×	×	CBT	
O. nigra, 1–27		×	×	CS	
O. obscura		×	×	CBT	
O. okeni		×	×	CBT	
O. proteus		×	×	CBT	
O. pseudogeminata		×	×	CBT	
O. quadripunctulata		×	×	CBT	
O. rubescens		×	×	CBT	
O. schultzii		×	×	CBT	
O. simplicissima		×	×	CBT	
O. splendida		×	×	CBT	
O. subbrevis		×	×	CBT	
O. tanganyikae		×	×	CBT	
O. tenuis		×	×	CBT	
O. tenuis var. *tergestina*		×	×	CBT	
O. trichoides		×	×	CBT	
Oscillatoria spp.		×	×	CBT	
Phormidium ambiguum		×	×	CBT	
P. anomala		×	×	CBT	
P. corium var. *constrictum*		×	×	CBT	
P. dimorphum		×	×	CBT	
P. mucosum		×	×	CBT	
P. retzii		×	×	CBT	
P. tenue		×	×	CBT	
Spirulina labyrinthiformis		×	×	CBT	
S. major, 1–27		×	×	CS	
S. subsalsa, 1–27		×	×	CS	
S. subtilissima		×	×	CBT	
Spirulina sp., 1–27		×	×	CS	
Symploca sp.				CBT	
Family Scytonemataceae					
Scytonema alatum	×	×		CBT	
S. rivulare	×	×		CBT	
Order Stigonemales					
Family Stigonemaceae					
Stigonema hormoides				CBT	

TABLE 1.3. *Continued*

	Substrate[b]				
Taxon[a]	V	M,S	G,R	Source[c]	Feeding Habits[d]
SUPERKINGDOM EUKARYOTAE					
KINGDOM PLANTAE					
Subkingdom Thallobionta					
Division Chlorophycota					
Order Chaetophorales					
Family Chaetophoraceae					
Cloniophora sp., 1–27				CS	
Stigoclonium flagelliferium, 1–27			×	CS	
S. pachydermum			×	CBT	
Stigoclonium sp., 1–27			×	CS	
Tetraedron sp., 1–27			×	CS	
Order Chlorococcales					
Family Chlorococcaceae					
Chlorococcum spp.	×	×		CBT	
Family Hydrodictyaceae					
Pediastrum boryanum	×	×		CBT	
P. duplex var. *clathratum*, 1–27	×	×		CS	
P. integrum	×	×		CBT	
P. integrum var. *scutum*	×	×		CBT	
Family Oocystaceae					
Cerasterias staurastroides, 1–27				CS	
Lagerheimie subsalsa, 1–27				CS	
Oocystis crassa		×		CBT	
O. elliptica		×		CBT	
O. solitaria		×		CBT	
Family Scenescedesmaceae					
Scenedesmus bijuga, 1–27		×		CS	
S. opoliensis, 1–27		×		CS	
S. quadricauda var. *maximus*, 1–27		×		CS	
Order Cylindrocapsales					
Family Cylindrocapsales					
Cylindrocapsa sp.				CBT	
Cylindrotheca gracilis				CBT	
Order Tetrasporales					
Family Tetrasporaceae					
Tetraspora cylindrica	×		×	CBT	
Tetraspora sp.	×		×	CBT	
Order Trentepohliales					
Family Trentepohliaceae					
Gongrosira lacustris				CBT	
Leptosira sp., 1–27				CS	
Trentepohlia aurea				CBT	
Order Ulotrichales					
Family Microsporaceae					
Microspora floccosa, 1–27			×	CS	
M. loefgrenii			×	CBT	
M. pachyderma			×	CBT	
Microspora sp.			×	CBT	
Ulothrix aequalis	×			CBT	
U. cylindricum	×			CBT	
U. subtilissima	×			CBT	
U. tenerrima	×			CBT	
U. tenuissima	×			CBT	

(continues)

TABLE 1.3. *Continued*

Taxon[a]	Substrate[b] V	M,S	G,R	Source[c]	Feeding Habits[d]
U. variabilis	×			CBT	
U. zonata	×			CBT	
Ulothrix sp., 1–27	×			CS	
Family Monostromataceae					
Gomontia sp., 1–27				CS	
Order Oedogoniales					
Family Oedogoniaceae					
Oedogonium spp.	×		×	CBT	
Order Cladophorales					
Family Cladophoraceae					
Cladophora fracta	×	×	×	CBT	
C. glomerata	×	×	×	CBT	
Rhizoclonium hieroglyphicum	×	×	×	CBT	
R. hookeri	×	×	×	CBT	
Order Zygnematales					
Family Desmidiaceae					
Closterium acerosum var. *elongatum*	×		×	CBT	
Closterium spp.	×		×	CBT	
Cosmarium spp.	×	×		CBT	
Staurastrum sp., 1–27		×		CS	
Family Zygnemataceae					
Mougeotia spp.	×		×	CBT	
Mougeotiopsis sp., 1–27	×		×	CS	
Spirogyra spp.		×	×	CBT	
Zygnema spp.			×	CBT	
Class Bacillariophyceae					
Order Eupodiscales					
Family Coscinodiscaceae					
Coscinodiscus denarius, 20			×	CBT	
Cyclotella atomus, 4	×	×	×	CBT	
C. meneghiniana, throughout Colorado River	×	×	×	CBT	
C. michiganiana, Lees Ferry, mile 19	×	×	×	CBT	
Melosira granulata, 18, 23	×	×	×	CM	
M. varians, widespread	×	×	×	CBT	
Order Biddulphiales					
Family Biddulphiaceae					
Biddulphia laevis, 15, 27	×		×	CBT	
Order Fragilariales					
Family Fragilariaceae					
Asterionella formosa, upper Colorado River			×	CBT	
Diatoma anceps, 1–27			×	CS	
D. elongatum, 1–27			×	CS	
D. hiemale, 1–27			×	CS	
D. hiemale var. *mesodon*, throughout Glen Canyon, especially 18			×	CB	
D. vulgare, widespread			×	CBT	
D. vulgare var. *breve*, 1, 11, 18, 19			×	CBT	
D. vulgare var. *linearis*, 14			×	CBT	
Fragilaria aequalis, 1–27				CS	
F. brevistriata, 1–27				CS	
F. brevistriata var. *inflata*, 9				CBT	
F. capucina, 15, 18, 23	×			CBT	
F. capucina var. *mesolepta*, 15, 23, 27	×			CBT	

TABLE 1.3. *Continued*

Taxon[a]	Substrate[b]			Source[c]	Feeding Habits[d]
	V	M,S	G,R		
F. construens, 1–27		×	×	CS	
F. construens var. *venter*, 27		×	×	CBT	
F. crotonensis, Lake Powell, upper Colorado River			×	CS	
F. intermedia, 1–27			×	CS	
F. leptostauron, 12, 18		×		CBT	
F. leptostauron var. *dubia*, 8		×		CBT	
F. vaucheriae, widespread	×	×	×	CBT	
F. virescens, 1–27		×		CS	
Meridion circulare, 15, 19, 27	×	×		CBT	
Opephora ansata, 25		×	×	CBT	
Synedra acus, common throughout Glen Canyon, abundant 13		×	×	CBT	
S. affinis, 15		×	×	CBT	
S. delicatissima var. *angustissima* upper Colorado River, probably remnant from Lake Powell			×	CBT	
S. goulardii, 18		×	×	CBT	
S. incisa, 18, 27		×	×	CBT	
S. mazamaensis, single collection at 11		×	×	CBT	
S. miniscula var. *longa*		×	×	CBT	
S. nana, 1–27			×	CS	
S. pulchella var. *lacerata*, 20	×	×	×	CBT	
S. rumpens	×		×	CBT	
S. rumpens var. *familiaris*, 21	×		×	CBT	
S. socia, widespread, high densities above little Colorado River		×	×	CBT	
S. tenera var. *genuina*, 1–27	×		×	CS	
S. ulna, widespread	×	×	×	CBT	
S. ulna var. *constracta*, 2	×	×	×	CBT	
Order Achnanthales					
Family Achnanthaceae					
Achnanthes affinis, widespread	×	×	×	CBT	
A. clevei, 1, 9	×	×	×	CBT	
A. coarctata, 6, 14	×	×	×	CBT	
A. deflexa, 15			×	CBT	
A. exigua var. *heterovalva*, widespread, especially 2		×	×	CBT	
A. flexella, Lees Ferry		×	×	CBT	
A. lanceolata, widespread in Glen Canyon	×	×	×		
A. lanceolata var. *dubia*, widespread in Glen Canyon	×	×	×	CBT	
A. lanceolata var. *omissa*, 19	×	×	×	CBT	
A. linearis, N., 1, 8, 12, 14, 18, 19, 20, 23	×	×	×	CBT	
A. linearis forma. *curvata*, widespread in Glen Canyon	×	×	×	CBT	
A. linearis var. *pusilla*, widespread in Glen Canyon	×	×	×	CBT	
A. microcephala, widespread in Glen Canyon		×	×	CBT	
A. minutissima, widespread	×	×	×	CBT	
A. sublaevis var. *crassa*, 1, 18, 19, 23	×	×	×	CBT	
A. wellsiae, mile 48.9	×	×	×	CBT	

(continues)

TABLE 1.3. *Continued*

Taxon[a]	Substrate[b] V	M,S	G,R	Source[c]	Feeding Habits[d]
Achnanthidium sp., 1–27				CS	
Cocconeis diminuta, 2, 12, 15, 19			×	CBT	
C. pediculus, widespread	×		×	CBT	
C. placentula, 12, 14, 18, 19, 23	×		×	CB	
C. placentula var. *euglypta*, widespread	×		×	CBT	
C. placentula var. *lineata*, widespread	×		×	CBT	
Rhoicosphenia curvata, widespread	×		×	CBT	
Order Naviculales					
Family Cymbellaceae					
Amphora adnata	×		×	CBT	
A. arizonica	×		×	CBT	
A. coffeiformis, 25	×		×	CBT	
A. ovalis, 6	×		×	CBT	
A. ovalis var. *pediculus*, widespread	×		×	CBT	
A. perpusilla, 8, 12, 18	×		×	CBT	
A. veneta, 27	×		×	CBT	
Cymbella affinis, widespread	×		×	CBT	
C. affinis var. *bipunctata*	×		×	CBT	
C. amphicephala, widespread	×		×	CBT	
C. aspera, 1–27	×		×	CS	
C. caespitosa var. *ovata*, 1–27	×		×	CS	
C. cistula, 15	×		×	CBT	
C. cymbiformis var. *nonpunctata*, 15	×		×	CB	
C. hungarica, 1–27	×		×	CS	
C. incerta, 1–27	×		×	CS	
C. laevis, widespread in small numbers	×		×	CBT	
C. leptoceros, 19	×		×	CBT	
C. magnapunctata	×		×	CBT	
C. mexicana	×	×		CBT	
C. microcephala, 1, 8, 12, 19, 23	×		×	CBT	
C. microcephala var. *crassa*, 1	×	×		CBT	
C. minuta, widespread	×		×	CBT	
C. norvegica, 6, 17	×		×	CBT	
C. parva	×		×	CBT	
C. prostata, widespread	×	×		CBT	
C. pusilla, 13, 15	×		×	CBT	
C. sinuata, 1	×	×		CBT	
C. tumida, widespread		×	×	CBT	
C. tumidula, 15		×	×	CBT	
C. turgida, 1–27			×	CS	
C. ventricosa, 1–27		×	×	CS	
C. ventricosa var. *semicircularis*, 1–27		×	×	CS	
Family Entomoneidaceae					
Entomoneis alata, 15, 27				CBT	
E. palludosa, 15, 27				CBT	
Family Gomphonemaceae					
Gomphoneis herculeana, widespread	×			CBT	
Gomphonema acuminatus	×			CBT	
G. affine, 3, 18, 23	×			CM	
G. affine var. *insigne*, 20	×			CBT	
G. grunowii, 23	×			CBT	
G. intracatum, 1, 15	×			CBT	
G. intracatum var. *vibrio*, 20	×			CBT	

TABLE 1.3. *Continued*

	Substrate[b]				
Taxon[a]	V	M,S	G,R	Source[c]	Feeding Habits[d]
G. olivaceum, 20	×			CBT	
G. parvulum, widespread	×			CBT	
G. subclavatum, widespread	×			CBT	
G. truncatum, widespread	×			CBT	
Family Naviculaceae					
Amphipleura pellucida, widespread		×		CBT	
Anomoeoneis exilis, 1–27		×		CS	
A. serians var. *brachysira*, 1–27		×		CS	
A. vitrea, 11, 27		×		CBT	
Caloneis amphisbaena, 23		×		CM	
C. bacillaris var. *thermalis*, 8, 10, 16		×		CBT	
C. bacillum, widespread		×		CBT	
C. backmanii, mile 19		×		CBT	
C. hyalina, 9		×		CBT	
C. pulchra var. *brevistriata* (= *C. silicula* var. *brevistriata*), 15		×		CBT	
C. silicula, 20		×		CM	
C. silicula var. *limosa*, 21		×		CM	
C. ventricosa var. *truncatula*, 20, 22		×		CBT	
Diploneis elliptica, 2	×			CBT	
D. oblongella, 2	×			CBT	
D. oculata, 2, 8	×			CBT	
D. puella, widespread	×			CBT	
D. smithii var. *dilatata*, 15	×			CBT	
Frustulia vulgaris, widespread		×	×	CB	
Gyrosigma spencerii, 20		×	×	CBT	
G. spencerii var. *curvula*, 6, 11, 15		×	×	CBT	
Mastagloia elliptica var. *danseii*, 15				CBT	
M. gravillei, 22				CBT	
M. smithii, widespread				CBT	
M. smithii var. *amphicephala*, 6, 11				CBT	
M. smithii var. *lacustris*, widespread				CBT	
Navicula accomoda, 12, 20		×		CBT	
N. angelica, 1–27		×		CS	
N. angelica var. *subsalsa*, widespread		×		CBT	
N. arvenensis, widespread		×		CBT	
N. bacillum, 11				CBT	
N. cari, 27				CB	
N. cincta, 9, 20		×		CBT	
N. cocconeiformis, 12				CBT	
N. confervaceae, 24	×		×	CB	
N. cryptocephala, widespread	×	×	×	CBT	
N. cryptocephala forma. *minuta*, widespread	×	×	×	CBT	
N. cryptocephala var. *veneta*, widespread	×	×	×	CBT	
N. cuspidata, sporadically observed throughout the Glen Canyon		×	×	CBT	
N. cuspidata var. *major*, 23		×	×	CBT	
N. decussis, widespread		×	×	CBT	
N. densestriata, 8				CBT	
N. dicephala		×		CBT	
N. eulineata				CBT	
N. exigua, 21		×		CB	
N. globulifera, 26				CB	

(continues)

TABLE 1.3. *Continued*

Taxon[a]	Substrate[b] V	M,S	G,R	Source[c]	Feeding Habits[d]
N. graciliodes, widespread		×		CB	
N. gregaria, 20		×		CBT	
N. grimmei, 20				CBT	
N. halophila, 15				CB	
N. lanceolata, 20, 23		×	×	CBT	
N. laterostrata, 23				CM	
N. longirostris, 9, mile 115				CBT	
N. minima, widespread			×	CBT	
N. miniradiata				CBT	
N. minuscula, 5, 21, 23				CBT	
N. mutica, widespread	×	×	×	CBT	
N. mutica var. *cohnii*, 13, 15, 18, 27	×	×	×	CBT	
N. mutica var. *stigma*, 15	×	×	×	CBT	
N. mutica var. *undulata*, 15	×	×	×	CBT	
N. notha, 3, 27				CBT	
N. pelliculosa, 20			×	CBT	
N. pseudoreinhardtii, 11, mile 134				CBT	
N. pupula, 23, 25, 26, mile 134		×		CBT	
N. pupula var. *capitata*, 1		×		CM	
N. pupula var. *rectangularis*, widespread		×		CBT	
N. radiosa, widespread	×	×		CBT	
N. radiosa var. *tenella*, widespread	×	×		CBT	
N. secreta var. *apiculata*, somewhat widespread, especially 12, 15			×	CBT	
N. seminulum var. *hustedtii*, 24		×		CB	
N. silicificata				CBT	
N. subtilissima, 2, 6		×		CBT	
N. symmetrica, 6, 23		×	×	CB	
N. tridentula, 6, 14				CBT	
N. tripunctata, widespread	×		×	CBT	
N. tripunctata var. *schizonemoides*, 6, 9	×		×	CBT	
N. tuscula, 1				CBT	
N. viridula, 8, 20, 21	×	×	×	CBT	
N. viridula var. *rostellata*, 23, 27	×	×	×	CBT	
N. zanoni, widespread, most common in 2, 14, 18				CBT	
Neidium binode, 15				CBT	
N. dubium, 1–27		×	×	CS	
N. dubium f. *constrictum*, 15, mile 19		×	×	CBT	
Pinnularia appendiculata, 20, 25		×		CBT	
P. borealis var. *rectangularis*, 15		×		CBT	
P. brebissoni, 19		×		CBT	
P. divergentissima, 6		×		CBT	
P. prescottii		×		CBT	
P. substomatophora, 24			×	CB	
Pinnularia sp., 1–27				CS	
Pleurosigma delicatulum, 15, 23				CBT	
Rhopalodia gibba, widespread				CBT	
R. gibba var. *ventricosa*, 15				CBT	
R. gibberula var. *vanheurckii*, widespread				CBT	
Scoliopleura peisonis, 15				CBT	
Stauroneis anceps, 15	×		×	CBT	
S. amphioxys var. *rostrata*	×		×	CBT	

TABLE 1.3. *Continued*

	Substrate[b]				
Taxon[a]	V	M,S	G,R	Source[c]	Feeding Habits[d]
S. smithii, 15	×		×	CBT	
Family Plagiotropidaceae					
Plagiotropis lepidoptera, 27				CBT	
Order Epithemiales					
Family Epithemiaceae					
Denticula elegans, widespread	×		×		CBT
D. rainerensis, 2, 4, others	×		×	CBT	
Epithemia adnata, 2, 6				CBT	
E. argus, 17, 28				CB	
E. argus var. *alpestris*, 2, 6				CBT	
E. argus var. *longicornis*, widespread				CBT	
E. sorex, widespread				CBT	
E. turgida, upper reaches of Colorado River, below Glen Canyon, but not in Lake Powell area				CBT	
Order Bacillariales					
Family Nitzschiaceae					
Bacillaria paradoxa, 27	×	×		CBT	
Hantzschia amphioxys, widespread	×			CBT	
H. amphioxys forma. *capitata*	×			CBT	
Nitzschia accedans, 12, 14, 15, 21				CB	
N. acicularis, widespread		×		CBT	
N. acicularis var. *closterioides*, 23		×		CB	
N. acuta, 14		×	×	CBT	
N. amphibia, widespread			×	CBT	
N. angustata, 8, 23; mile 34.5				CBT	
N. angustata var. *acuta*, 14, 20				CBT	
N. apiculata, widespread	×			CBT	
N. bicrena, 14				CBT	
N. bita, 15				CBT	
N. capitellata, 20		×	×	CBT	
N. communis, widespread				CBT	
N. denticulata, 2				CBT	
N. dissipata, widespread	×	×	×	CBT	
N. filiformis, 12, 21	×	×		CB	
N. fonticola, 20				CBT	
N. frustulum, widespread	×	×	×	CBT	
N. frustulum var. *perpusilla*, 18	×	×	×	CBT	
N. gracilis, 15				CBT	
N. hungarica, 20				CBT	
N. hybrida, 19				CBT	
N. kutzingiana, widespread			×	CBT	
N. lacunarum, 4				CBT	
N. linearis, widespread				CBT	
N. littoralis var. *tergestina*, 20				CBT	
N. microcephala				CBT	
N. palea, 1, 12, 18, 19, 20, 23	×	×	×	CBT	
N. parvula, 23				CB	
N. pseudolinearis				CBT	
N. recta, 23				CBT	
N. romano, 2, 12, 15		×		CM	
N. scalpelliforma				CBT	
N. sigma, 8, 19, 20	×		×	CBT	

(continues)

TABLE 1.3. *Continued*

	Substrate[b]				
Taxon[a]	V	M,S	G,R	Source[c]	Feeding Habits[d]
N. sigmoidea, 15				CB	
N. sinuata var. *tabellaria*, 14				CBT	
N. tryblionella var. *calida*, 20, 23		×		CBT	
N. tryblionella var. *levidensis*, 21, 23		×		CB	
N. vermicularis, 14			×	CBT	
Nitzschia spp., 1, 8, 12, 19, 23					
Order Surirellales					
Family Surirellalaceae					
Campylodiscus noricus var. *hibernica*, 2				CBT	
Cymatopleura solea, 15		×		CBT	
Surirella angustata, widespread		×		CBT	
S. brightwellei, widespread		×		CBT	
S. ovalis, 8				CBT	
S. ovata, widespread, esp. 20		×		CBT	
S. ovata var. *africana*, 14		×		CBT	
S. ovata var. *pinnata*, 20		×		CBT	
S. patella, 22				CBT	
S. striatula, 11, 15, 27		×		CBT	
S. striatula var. *parva*		×		CBT	
Division Rhodophycota					
Class Rhodophyceae					
Order Nemalionales					
Family Batrachospermaceae					
Batrachospermum sp.			×	CBT	
Division Chromophycota					
Class Xanthophyceae					
Tetragoniella sp., 1–27				CS	
Order Vaucheriales					
Family Tribonemataceae					
Tribonema utriculosum, 1–27				CS	
Family Vaucheriaceae					
Vaucheria geminata				CBT	
V. sessilis				CBT	
Vaucheria spp.				CBT	
Class Dinophyceae					
Order Peridinales					
Family Ceratiaceae					
Ceratium carolinianum, 1–27			×	CS	
C. hirudinella, 1–27			×	CS	
Subkingdom Embryobionta					
Division Magnoliophyta					
Class Magnoliopsida					
Subclass Dilleniidae					
Order Malvales					
Family Malvaceae					
Iliamna grandiflora				CM	
Sida nederacea				CM	
Sidalcea neomexicana				CM	
Order Theales					
Family Elatinaceae					
Elatine brachysperma				CM	
E. triandra				CM	

TABLE 1.3. *Continued*

	Substrate[b]				
Taxon[a]	V	M,S	G,R	Source[c]	Feeding Habits[d]
Family Guttiferae					
Hypericum anagalloides				CM	
H. formosum				CM	
Order Violales					
Family Loasaceae					
Eucidne urens				CM	
Family Tamaricaceae					
Tamarix aphylla				CM	
T. pentandra				CM	
Order Primulales					
Family Primulaceae					
Androsace occidentalis				CM	
A. septentrionalis				CM	
Dodecatheon alpinum				CM	
Samolus parviflorus				CM	
Subclass Rosidae					
Order Proteales					
Family Elaeagnaceae					
Elaeagnus angustifolia				CM	
Order Myrtales					
Family Onagraceae					
Epiloium adenocaulon				CM	
E. halleanum				CM	
E. hornemanni				CM	
E. saximontanum				CM	
Oenothera flava				CM	
O. hookeri				CM	
O. longissima				CM	
Order Apiales					
Family Umbrelliferae (= Apiaceae)					
Berula erecta				CM	
Caucalis microcarpa				CM	
Cicuta douglasii				CM	
Conium maculatum				CM	
Perideridia parishii				CM	
Order Cornales					
Family Cornaceae					
Cornus stolonifera				CM	
Subclass Asteridae					
Order Scrophulariales					
Family Oleaceae					
Fraxinus anomala				CM	
F. cuspidata var. *macropetala*				CM	
F. pennsylvanica velutina				CM	
Order Gentianales					
Family Apocynaceae					
Apocynum cannabinum				CM	
A. sibiricum var. *salignum*				CM	
A. suksdorfii				CM	
Family Asclepiadaceae					
Asclepias subverticillata				CM	
Sarcostemma cynanchoides				CM	
Family Gentianaceae					
Centarium calycosum				CM	

(continues)

TABLE 1.3. *Continued*

	Substrate[b]				
Taxon[a]	V	M,S	G,R	Source[c]	Feeding Habits[d]
Gentiana affinis				CM	
G. parryi				CM	
Order Solanales					
Family Convolvulaceae					
Convolvulus arvensis				CM	
Cuscuta campestris				CM	
C. coryli				CM	
C. indecora				CM	
Family Hydrophyllaceae					
Phacelia magellanica				CM	
Family Polemoniaceae					
Collomia linearis				CM	
Family Solanaceae					
Datura meteloides				CM	
Nicotiana glauca				CM	
N. trigonophylla				CM	
Solanum douglasii				CM	
S. nodiflorum				CM	
Order Lamiales					
Family Boraginaceae					
Hackelia floribunda				CM	
Heliotropium curassavicum				CM	
Lappula redowskii				CM	
Mertensia franciscana				CM	
Family Labiatae (= Lamiales)					
Mentha arvenis var. *villosa*				CM	
M. spicata				CM	
Nepeta cataria				CM	
Prunella vulgaris				CM	
Family Verbenaceae					
Phyla cuneifolia				CM	
Verbena bractea				CM	
V. macdougalii				CM	
Order Scrophulariales					
Family Scrophulariaceae					
Besseya arizonica				CM	
B. plantaginea				CM	
Castilleja confusa				CM	
Limosella acaulis				CM	
L. aquatica				CM	
Maurandya antirrhiniflora				CM	
Mimulus cardinalis				CM	
M. guttatus				CM	
M. nasutus				CM	
M. primuloides				CM	
M. rubellus				CM	
Penstemon rydbergii				CM	
P. virgatus				CM	
Penstemon sp.				CM	
Veronica americana				CM	
V. anagallis-aquatica				CM	
V. serphyllifolia var. *borealis*				CM	

TABLE 1.3. *Continued*

	Substrate[b]				
Taxon[a]	V	M,S	G,R	Source[c]	Feeding Habits[d]
Order Plantaginales					
Family Plantaginaceae					
Plantago insularis				CM	
P. lanceolata				CM	
P. major				CM	
P. virginica				CM	
Order Rubiales					
Family Rubiaceae					
Galium stellatum var. *eremicum*				CM	
G. tinctorium				CM	
G. triflorum				CM	
Hedyotis pygmaea (= *Houstonia wrightii*)				CM	
Order Dipsacales					
Family Carpifoliaceae					
Sambucus glauca				CM	
S. microbotrys				CM	
Family Valerianaceae					
Valeriana capitata				CM	
V. edulis				CM	
V. occidentalis				CM	
Order Campanulales					
Family Campanulaceae					
Campanula parryi				CM	
C. rotundifolia				CM	
Lobelia anatina				CM	
L. cardinalis graminea				CM	
Order Asterales					
Family Compositae (= Asteraceae)					
Achillea millefolium var. *lanulosa* (= *A. lanulosa*)				CM	
Agoseris aurantiaca				CM	
A. glauca				CM	
Ambrosia psilostachya				CM	
Arnica chamissonis (= *A. foliosa*)				CM	
Artemisia biennis				CM	
A. tridentata				CM	
Aster adscendens				CM	
A. foliaceus				CM	
A. intricatus				CM	
A. spinosus				CM	
Baccharis emoryi				CM	
B. salicifolia (= *B. glutinosa*)				CM	
B. sarathroides				CM	
B. viminea				CM	
Bidens tenuisecta				CM	
Chrysothamnus nauseosus				CM	
Cichorium intybus				CM	
Cirsium nidulum				CM	
Cirsium sp.				CM	
Conyza canadensis (= *Erideron canadensis*)				CM	
Flaveria mcdougallii				CM	
Franseria confertifolia				CM	
Gnaphalium chilense				CM	
G. exilifolium (= *G. grayi*)				CM	
G. palustre				CM	

(continues)

TABLE 1.3. *Continued*

	Substrate[b]				
Taxon[a]	V	M,S	G,R	Source[c]	Feeding Habits[d]
Haplopappus acradenius				CM	
Helianthus ciliaris				CM	
Lactuca pulchella				CM	
L. serriola				CM	
Perityle emoryii				CM	
Solidago altissima				CM	
S. ana				CM	
S. decumbens				CM	
S. occidentalis				CM	
Sonchus asper				CM	
S. oleraceus				CM	
Stephanomeria pauciflora				CM	
Taraxcum officinale				CM	
Tessaria sericea (= *Plucea sericea*)				CM	
Verbesina enceloides				CM	
Xanthium strumarium (= *X. saccharatum*)				CM	
KINGDOM ANIMALIA					
Subkingdom Protozoa					
Class Mastigophora					
Order Cryptomonadida					
Family Cryptomonadidae					
Cryptomonas ovata, 1–27				CS	O
Order Chrysomonadida					
Family Ochromonadidae					
Dinobryon sertularia, 1–27		×	×	CS	O
Order Phytomonadida					
Family Carteridae					
Carteria klebsii, 1–27				CS	O
Family Chlamydomonidae					
Chlamydomonas sp., 1–27	×	×		CS	O
Family Volvacidae					
Pandorina morum, 1–27		×		CS	O
Order Euglenoidida					
Family Euglenidae					
Colacium sp., 1–27				CS	O
Trachelomas sp., 1–27				CS	O
Phylum Annelida					
Class Enchytraeidae, 1, 2, 8					
Class Hirudinoidae, 2, 12, 25					
Class Lumbricidae, 2, 12, 25					
Family Lumbriculidae					
Class Oligochaeta					
Order Haplotaxida					
Family Naididae					
Chaetogaster diaphanus, 1	×	×	×	BSS	C
Nais communis, 1	×	×	×	BSS	O
N. elinguis, 1, 2, 8; mile 51.6	×	×	×	BSS	O
N. pardalis, 1; mile 51.6	×	×	×	BSS	O
N. pseudobtusa, 2	×	×	×	BSS	O
N. variabilis, 1, 2, 8	×	×	×	BSS	O
Nais sp., 2; mile 51.6	×	×	×	BSS	O
Ophidonais serpentina, 1	×			BSS	O

TABLE 1.3. *Continued*

	Substrate[b]				
Taxon[a]	V	M,S	G,R	Source[c]	Feeding Habits[d]
Pristina sp., 1	×			BSS	O
Family Tubificidae					
Limnodrilus hoffmeisteri, 2, 12; mile 51.6		×		BSS	O
Tubifex tubifex, 1, 2; mile 51.6		×		BSS	O
Phylum Mollusca					
Order Basomatophora					
Class Gastropoda					
Family Cochlicopidae					
Cionella lubrica, 12, 18	×	×		SB	HD
Family Discidae					
Discus cronkhitei, 18	×	×		SB	HD
Family Helicarionidae					
Euconulus fulvus, 12	×	×		SB	HD
Family Helminthoglyptidae					
Sonorella coloradoensis, 12	×	×		SB	HD
Family Limacidae					
Deroceras laeve	×	×		SB	HD
Family Lymnaeidae					
Fossaria obtussa, 1, 2; 8, mile 51.6	×	×		SB	HD
F. parva	×	×		SB	HD
Family Oreohelicidae					
Oreohelix yavapai, 12	×	×		SB	HD
Family Planoboridae					
Gyraulus parvus		×		SB	HD
Family Physidae					
Physella humerosa, 12	×	×	×	SB	C
P. osculans, 12	×	×	×	SB	C
P. squalida, 12	×	×	×	SB	C
P. virgata virgata	×	×	×	SB	C
Physella sp., 1–25	×	×	×	SB	C
Family Pupillidae					
Gastrocopta ashmuni, 12	×	×		SB	HD
G. pelliculida	×	×		SB	HD
G. pilsbryana, 12	×	×		SB	HD
Pupilla blandi	×	×		SB	HD
P. hebes	×	×		SB	HD
P. syngenes	×	×		SB	HD
Pupilla sp.	×	×		SB	HD
Pupoides hordacea	×	×		SB	HD
P. nitidulus	×	×		SB	HD
Family Succineidae					
Catinella avara, 12, 13, 14, 18	×	×		SB	HD
Oxyloma haydeni kanabensis, 2	×	×		SB	HD
Succinea grosvenorii	×	×		SB	HD
Family Thysanophoridae					
Microphysula ingersolii	×	×		SB	HD
Thysanophora hornii	×	×		SB	HD
Family Valloniidae					
Vallonia cyclophorella, 12	×	×		SB	HD
V. perspectiva, 12	×	×		SB	HD
Family Vitrinidae					
Vitrina alaskana	×	×		SB	HD

(continues)

TABLE 1.3. *Continued*

Taxon[a]	Substrate[b] V	M,S	G,R	Source[c]	Feeding Habits[d]
Family Zonitidae					
Glyphyalinia indentata, 12	×	×		SB	HD
Hawaiia miniscula, 2	×	×		SB	HD
Zonitoides arborus	×	×		SB	HD
Order Veneroida					
Class Bivalvia					
Family Sphaeridae					
Pisidium variabile, 1		×		SB	HD
P. walkeri, 1					HD
Class Crustacea					
Subclass Cephalocardia					
Order Calanoida					
Family Diaptomidae					
Aglaodiaptomus clavipes		×		H	O
A. forbesi		×		H	O
Diaptomus sp.		×		H	O
Leptodiaptomus ashlandi		×		H	O
L. sicilis		×		H	O
Skistodiaptomus pallidus		×		H	O
S. reighardi		×		H	O
Order Cladocera					
Family Bosminidae					
Bosmina longirostris		×		H	OD
Family Chydoridae					
Alona affinis		×		H	OD
A. guttata		×		H	OD
Chydorus sphaericus		×		H	OD
Leydigia quadrangularis		×		H	OD
Pleuroxis aduncus		×		H	OD
P. denticulatus		×		H	OD
Family Daphnidae					
Daphnia galeata mendotae	×	×		H	OD
D. parvula	×	×		H	OD
D. pulex	×	×		H	OD
Daphnia sp.	×	×		H	OD
Diaphanosoma birgei	×	×		H	OD
Subclass Copepoda					
Order Cyclopodia					
Family Cyclopodae					
Acanthocyclops vernalis	×	×		H	OD
Diacyclops thomasi	×	×		H	OD
Eucyclops agilis	×	×		H	OD
E. speratus	×	×		H	OD
Mesocyclops edax	×	×		H	OD
Paracyclops fimbriatus poppei	×	×		H	OD
Tropocyclops prasinus mexicanus	×	×		H	OD
Order Harpacticoida					
Unident sp.		×		H	
Order Amphipoda					
Family Gammaridae					
Gammarus lacustris, 1–25	×	×		H	O
Subclass Ostracoda					
Order Podocopina					
Family Cypridae					

TABLE 1.3. *Continued*

	Substrate[b]				
Taxon[a]	V	M,S	G,R	Source[c]	Feeding Habits[d]
Cypridopsis incongruens		×		H	O
C. pellucidus		×		H	O
C. salinus		×		H	O
C. vidua		×		H	O
Herpetocypris reptans	×	×	×	H	O
Ilyocypris bradyii				H	O
Paracandona euplectella				H	O
Potamocypris sp.				H	O
Class Insecta					
Order Diptera					
Family Chironomidae					
Apedilum subcinctum				BSS	
Cardiocladius platypus, 1, 8, 12, 21, 22; miles 51.6, 64.5, 183			×	BSS	C
Chironomus utahensis, 1	×	×		BSS	OH
Chironomus sp., 8, 12, 25; mile 51.6	×	×		BSS	OH
Cladotanytarsus sp., 8, 12, 25; 51.6 mile	×	×		BSS	O
Cricotopus annulator, 1–25	×	×	×	BSS	O
C. globistylus, 1, 12; 51.6 mile	×	×	×	BSS	O
C. infuscatus, miles 64.5, 193	×	×	×	BSS	O
C. trifascia, 8, 12, 20, 21, 22; miles 51.6, 64.5, 193	×	×	×	BSS	O
Cricotopus sp., 1, 2, 12, 20, 21, 22; mile 51.6	×	×	×	BSS	O
Cyphomella gibbera, 8, 12; mile 193				BSS	
Diamesa heteropus, 8			×	BSS	O
Eukiefferiella claripennis, 1–25	×	×	×	BSS	OC
E. coerulescens, 1–12	×	×	×	BSS	OC
E. devonica, 21, 22; mile 64.5	×	×	×	BSS	OC
E. ilkleyensis, 1–mile 193	×	×	×	BSS	OC
Eukiefferiella spp., 1	×	×	×	BSS	OC
Limnohyphes sp., 20	×	×	×	BSS	O
Metriocnemus sp., mile 51.6	×	×	×	BSS	OC
Micropsectra sp., 1	×	×		BSS	O
Orthocladius consobrinus, 20	×	×	×	BSS	HD
O. frigidus, 1	×	×	×	BSS	HD
O. luteipes, 2	×	×	×	BSS	HD
O. mallochi, mile 193	×	×	×	BSS	HD
O. rivicola, 1–25	×	×	×	BSS	HD
Parakiefferiella sp., 2, 12, 20	×	×	×	BSS	O
Paraphaenocladius exagitans, 3	×	×	×	BSS	O
Phaenopsectra profusa, 8, 21, 22, 25; mile 51.6	×	×		BSS	O
Polypedilum apicatum, mile 193	×			BSS	O
P. obelos, 8, 12, 21, 22; miles 51.6 193	×			BSS	O
Pseudosmitta sp., 2			×	BSS	O
Rheotanytarsus spp., 20			×	BSS	O
Tvetenia discoloripes				BSS	O
Family Simuliidae					
Simulium arcticum, 1–25			×	BSS	O
S. argus, 20, 21, 22; mile 193			×	BSS	O
S. griseum, 25			×	BSS	O
S. petersoni, 25			×	BSS	O

(continues)

TABLE 1.3. *Continued*

Taxon[a]	Substrate[b] V	Substrate[b] M,S	Substrate[b] G,R	Source[c]	Feeding Habits[d]
S. vittatum, 1			×	BSS	O
Family Tipulidae					
Order Trichoptera					
Order Hemiptera					
Family Corixidae					
Graptocorixa serrulata	×	×		PP	C
Family Gelastrocoridae					
Gelastocoris oculatus	×	×		PP	C
Family Gerridae					
Gerris remigis		×	×	PP	C
Family Hebridae					
Hebrus hubbardi	×			PP	C
H. obscura	×			PP	C
Family Macroveliidae					
Macrovelia hornii		×	×	PP	C
Family Notonectidae					
Notonecta lobata	×	×		PP	C
Family Ochteriae					
Ochterus barberi	×		×	PP	C
O. rotundus	×		×	PP	C
Family Saldidae					
Saldula pallipes		×	×	PP	C
S. pexa		×	×	PP	C
Family Veliidae					
Microvelia beameri		×	×	PP	C
M. torquata		×	×	PP	C
Rhagovelia distincta			×	PP	C
Phylum Chordata					
Subphylum Vertebrata					
Class Osteichthyes					
Order Cypriniformes					
Family Catostomidae					
Catostomus latipinnis, widespread		×	×	CBT	O
Pantosteus (*Catostomus*) *discobolus*, widespread		×	×	CBT	O
Xyrauchen texanus, 1		×	×	CBT	O
Order Cypriniformes					
Family Cyprinidae					
**Cyprinus carpio*, widespread	×	×		CBT	O
Gila cypha, 8	×	×	×	CBT	O
G. elegans	×	×	×	CBT	O
G. robusta	×	×	×	CBT	O
**Lepidomeda mollispinis*				CBT	O
**Notemigonus crysoleucus*	×	×		CBT	C
**Notropis lutrensis*		×		CBT	O
**Pimephales promelas*, widespread		×		CBT	O
**Plagopterus argentissimus*				CBT	
Ptychocheilus lucius		×		CBT	C
Rhinichthys osculus, widespread		×		CBT	O
Order Salmoniformes					
Family Salmonidae					
**Oncorhynchus kisutch*			×	CBT	C
**Salmo clarki*			×	CBT	C

TABLE 1.3. *Continued*

	Substrate[b]				
Taxon[a]	V	M,S	G,R	Source[c]	Feeding Habits[d]
**S. gairdneri*, widespread			×	CBT	C
**S. trutta*, widespread			×	CBT	C
**Salvelinus fontinalis*, widespread			×	CBT	C
Order Siluriformes					
Family Ictaluridae					
**Ictalurus melas*		×		CBT	O
**I. punctatus*, 8, 20		×		CBT	O
Order Cyprinodontiformes					
Family Cyprinodontidae					
**Fundulus zebrinus*, 10, 20, Royal Arch		×		CBT	O
Order Perciformes					
Family Centrarchidae					
**Micropterus salmoides*	×	×		CBT	C
**Chaenobryttus* (= *Lepomis*) *cyanellus*	×	×		CBT	C
**Lepomis macrochirus*	×	×	×	CBT	O
Family Percichthidae					
**Morone saxatilis*			×	CBT	C
Family Percidae					
**Stizostedion vitreum*	×	×	×	CBT	C

[a]An asterisk indicates an introduced species. Numbers indicate the sites where the samples were collected.
[b]V, vegetation and debris; M, mud; S, sand; G, gravel; R, rubble.
[c]BSS, Blinn et al. (1992); CB, Czarnecki and Blinn (1978); CBT, Czarnecki et al. (1976); CM, Carothers and Minckley (1981b); CS, Crayton and Sommerfeld (1978); H, Haury (1986); PP, Polhemus and Polhemus (1976); SB, Spamer and Bogan (1993).
[d]Feeding habits: C = carnivore; HD = herbivore-detritivore; O = omnivore; OC = omnivore-carnivore; OD = omnivore-detritivore; OH = omnivore-herbivore.

boulders at Nankoweap (between river miles 51 and 52) because there was intense sandblasting of the boulders by sand carried in the strong current. The increase in *Cladophora glomerata* seemed to be correlated with channel depth at sites above Lees Ferry. Similarly, there was a decrease in biomass with depth at sites below Lees Ferry. The decrease in *Cladophora glomerata* at greater depths of the channel may have been due largely to the rapid attenuation of light due to periodically high sediment loads.

Large standing crops of *Cladophora glomerata* were found to be a habitat for the amphipod *Gammarus lacustris* and other small invertebrates. It also provided an enormous surface area for the attachment of epiphytic diatoms, which are an important food for aquatic invertebrates and in some cases for fish. Two hundred and thirty-five periphytic diatoms were reported by Czarnecki and Blinn (1978) in the seeps, in the mouths of tributaries, and in the Colorado River in the Grand Canyon reach. The greatest abundance of attached algae occurred in the summer months from June and July. Of the total number of taxa, 65% were diatoms, 24% cyanobacteria, and 10% chlorophytes. At the confluence of Diamond Creek a red algae, *Batrachospermum* sp., was reported. Another red alga that was present was *Audouienella* sp., often attached to the filaments of *Cladophora glomerata* and found in the deeper sections of the river channel.

Two hundred and thirty-five diatom taxa were also found in this reach of the river between the Marble and Grand Canyon systems. Here the dominant taxa were *Diatoma vulgare*, *Synedra ulna*, and *Cocconeis pediculus*. *Diatoma vulgare* and *Synedra ulna* were present in about the same amount before the impoundment. However, *Cocconeis pediculus* has increased in relative importance since impoundment. Their increase may indicate that *Cladophora glomerata* has also increased since the closure of Glen Canyon Dam. Usher et al. (1987) found that *Achnanthes affinis*, *Cocconeis pediculus*, *Diatoma vulgare*, and *Rhoicosphenia curvata* made up 80% of the communities upstream from Lees Ferry, whereas these four taxa were much less important at downstream sites, and *Gomphonema olivaceum*, *Cymbella affinis*, and *Nitzschia dissipata* became more important at the downstream sites. It may be that the change in species composition was due to their tolerance to suspended sediments (Bahls et al., 1984; Lowe, 1974).

Below Lees Ferry there was a fourfold decrease in epiphytic diatoms compared with sites above Lees Ferry, which corresponds to a decrease in cell density with increasing channel depth. The two patterns of diatom occurrence may both relate to the amount of suspended sediments, water depth, and light attenuation.

Invertebrates

It is difficult to compare the aquatic invertebrates before and after dam closure because of the introduction of many individuals of insects, snails, and leeches. Zooplankton and the algae seemed to be derived from lentic populations in Lake Powell. Haury (1986) proposed that occasional releases of surface water from spillways would enhance river populations, and nocturnal releases would have the greatest influence. Cladocera and copepods would rise temporarily due to the pattern of releases. There is evidence that the microcrustaceans below the dam increased to at least the mouth of Diamond Creek about 388 km below Glen Canyon Dam. However, Haury notes that the percentage of copepod planktors in poor condition increased downstream. Of the 34 invertebrates listed by Haury, only 16 were true planktors. The others were benthic. However, they sometimes break loose and drift downstream and are sampled in the plankton. These drifters contributed most of the biomass. Other planktors listed by Kubly (1976) were rotifers, a collembolan, and water mites. The last two are characterized best as epineustonic. The mites are probably nectonic. We can only speculate as to the origin of some of the crustacean planktors. *Aglaodiaptomus clavipes* and *Leptodiaptomus sicilis* were found in Lake Mead.

The backwaters that occurred along the borders of the river channel and at the mouths of tributaries are refugia for a rich fauna of invertebrates. There seemed to be a higher productivity of these invertebrates in the backwaters. The viability of these backwaters as habitats in the main stream of the Colorado River was also noted during a 1987–1989 survey (Kubly, 1976). Kubly noted a greater abundance in the quiet backwaters than in the main stream. The relative abundance of the Cladocera may be due to the preference of habitat but may also be due to the relative amount of fish predation.

Most sites for aquatic life are located near the mouths of tributaries and around debris caught in the river at the Grand Canyon National Park and vicinity. Just below the Glen Canyon Dam, the current is stochastic and the water is generally clear and deep. The rapid flow inhibits many types of organisms. Debris caught within the channel of the Grand Canyon and along the edges of the channel and at the mouths of tributaries furnish habitats for most of the aquatic life.

The vegetation ecosystem consists of algae and submerged leaves and stems of vascular plants—some mosses are also present. The Nostocaceae associated with this habitat were *Nostoc hatei*, *N. paludosum*, *N. punctiforme*, *N. verrucosum*, and unidentified species of *Nostoc*. Also present in this habitat was *Gloeotrichia intermedia*, which belongs to the family Oscillatoriaceae. Two algae that are members of the family Scytonemataceae, *Scytonema alatum* and *S. rivulare*, were also present; as was one member of the family Chlorococcaceae, species belonging to the genus *Chlorococcum*; and four taxons belonging to the family Hydrodictyaceae, all belonging to the genus *Pediastrum*. Other algae present were two taxons belonging to the genus *Tetraspora* of the order Tetrasporales. The green algae belonging to the order Ulotrichales were represented by one taxon belonging to the genus *Microspora* and seven taxons belonging to the genus *Ulothrix*. The family *Oedogoniaceae* was represented by unidentified species of the genus *Oedogonium*. Other species of green algae found associated with vegetation were two taxons belonging to the genus *Cladophora* and two belonging to the genus *Rhizoclonium* (Table 1.3).

The desmids were represented by three taxons belonging to the genera *Closterium* and *Cosmarium*. The family Zygnemataceae was represented by species belonging to the genus *Mougeotia* and one species belonging to the genus *Mougeotiopsis*. Diatoms were commonly found associated with the vegetation. They lived in and among the filaments of other algae or associated with the leaves of higher plants. They were three species belonging to the genus *Cyclotella* and two species belonging to the genus *Melosira*. Also present was one species, *Biddulphia laevis*, belonging to the family Biddulphiaceae. The family Fragilariaceae was represented by three taxons belonging to the genus *Fragilaria*. Also present were *Meridion circulare* and six taxons belonging to the genus *Synedra*. The genus *Achnanthes* was represented in this habitat by 12 taxons, the genus *Cocconeis* by four taxons, and the genus *Rhoicosphenia* by one taxon. The family Cymbellaceae was represented by seven taxons belonging to the genus *Amphora*, and the genus *Cymbella* was represented by 21 taxons. These two genera typically grow attached to substrates and therefore were probably attached to the stems or leaves of submerged plants or to the filaments of algae. The family Gomphonemaceae typically grow attached to algae or stems or leaves of plants or mosses. Eleven taxons were found in this habitat in this reach of the river (Table 1.3).

Associated with the algal filaments, or with plant debris, or in some cases with submerged aquatic plants were five taxons belonging to the genus *Diploneis*. The genus *Navicula*, which is typically found enmeshed but sometimes loosely attached to the vegetative substrates, was represented by 14 taxons. Associated with the vegetation were three taxons belonging to the genus *Stauroneis* and two taxons belonging to the genus *Denticula*. Also present within the vegetation were several members of the family Nitzschiaceae: *Bacillaria paradoxa*, *Hantzschia amphioxys*, and *H. amphioxys* f. *capitata*, and seven taxons belonging to the genus *Nitzschia* (Table 1.3).

A green alga, *Cladophora glomerata*, has become established on the riverbed as a result of increased light penetration and greater stability of the riverbed (Dolan et al., 1974; Blinn and Cole, 1991). Large seasonal extremes in discharged sediment load and temperature seem to have been eliminated since construction of the Grand Canyon Dam.

The discharge is now regulated by regional power demands. The maximum is about 566 cm s^{-1} and the daily minimum is 130 cm s^{-1} with extremes ranging from 28 to 764 cm s^{-1}. Water entering the river from near the base of the dam is clear and cold, the temperature ranging from 15 to 60°F (–9.5 to 15.56°C). The river is cooler in summer and warmer in winter than in predam days.

Invertebrate Fauna

The main-stem invertebrates of the Colorado River were generally low in productivity (biomass and density per square meter) except possibly in the section between Glen Canyon Dam and the confluence of the Little Colorado River, where the sediment input was minimal. Here the estimates of density were several thousand individuals per square meter. In contrast, grab samples taken below the confluence with the Little Colorado River usually yielded only 5 to 10 individuals m^{-2}. These were blackflies, midges, and aquatic earthworms, which were collected in exposed gravel bars in the stream channel and along the margins of the river (Table 1.3).

The density of invertebrates seemed to be lower at the confluence of the tributaries. Insects were fewer in spring and summer. In the Paria River, Elves Chasm, and Kanab Creek, there was little similarity between upstream and stations at the confluence with the Colorado River. This may be related to the difference in substrate type between the confluence and the upstream sampling areas. The tributaries seem to be most similar to each other in the spring. Only Hermit Creek deviated from this pattern. Compared with tributaries and other riverine systems, the reduced productivity in the main stream of the Colorado River seems to be due to the cooler annual temperature and the greater depth, the current velocity, and sediment input.

The colder annual temperatures reduce growth rates and hence the number of generations produced per year. Because of the hypolimnion water released from Glen Canyon Dam, the temperature was stressed in the river for many miles downstream and affected the invertebrate communities, resulting in less productivity and diversity. Some of the tributaries, such as the Little Colorado River, carried a great deal of sediment into the Colorado River proper, and this reduced light penetration and hence primary and secondary productivity. The reach between the Glen Canyon Dam and the Little Colorado River has the least input of sediments and hence has an increase in invertebrate productivity and diversity.

Common invertebrates in the main stream were freshwater amphipods and aquatic earthworms. These species were able to exist and reproduce in these habitats, whereas this was not possible with other invertebrates. In general the invertebrate biomass and density in the Colorado tributaries were substantially less than those in other streams in the Southwest (Oberlin et al., 1999). Several factors seemed to contribute to the low productivity of these tributaries. The high canyon walls to the north and south and the topographic variability combined to create a formidable dispersal barrier for many aquatic species. The canyon topography has effectively blocked the northward dispersal of some species that are present 128 km south of Oak Creek Canyon. As a result, the aquatic Hemiptera fauna, like other invertebrate orders in the canyon, is typical of the Southwest, although it is depaupered compared with collections made in other areas of Arizona that are similar to the canyon in habitat diversity and topography. Emergent forms of many aquatic insects are short-lived and wingless or poor flyers, such as the mayflies, stoneflies, dragonflies, damselflies, and water striders, which further reduces their dispersal ability.

Productivity and diversity were lowest in the spring and summer. It is probable that the spring runoff and summer flash floods from the tributaries disrupt the benthic invertebrate communities by washing out many species. This probably results in the similarity of the fauna in the tributaries. Flooding also reduces the algae populations on which many invertebrates depend. The small amount of flooding in fall and winter favored increased algae and invertebrate productivity in these seasons. Inactivity may also bring about a decrease in summer invertebrate populations in the tributaries. This is because the substrate is unstable, caused by streambed alterations, and thus would increase the drift of the insects. The water levels are high in the main stream of the Colorado River when the water at the confluence of each tributary is more similar to that of the main stream with regard to temperature, chemistry, suspended solids, sediments, and discharge, thus increasing the similarity between the fauna of the tributary and the main stream. The main stream of the Colorado River is typically cooler than that of the tributaries, and this may have a great influence on the invertebrate fauna. Furthermore, turbidity and suspended solids were higher in the main stream than in the tributaries: 986 mg L^{-1} and 170 JTU (Jackson turbidity units), respectively, in the main stream; 100 mg L^{-1} and 30 JTU in the tributaries (Cole and Kubly, 1976).

It is undoubtedly a combination of unstable physical and chemical parameters that reduces the fauna in the mouths of the tributaries and in the Colorado River just below the entrance of the tributaries. In general, the benthic invertebrate productivity in the Colorado River was lower than in the tributaries and in other rivers in the Southwest. It is believed to be due to the river's cooler annual temperature, greater depth, current velocity, and sediment input. In general, the areas that supported the richest invertebrate fauna were in rare shallow backwaters, eddies, along the margins of the river, and in the river section between Glen Canyon Dam and the Little Colorado River. Invertebrate groups found in the main stem were also present in various habitats in the tributaries. In general, the intratributary comparisons of the benthic invertebrate communities show that productivity and diversity were generally lower at the confluence. The physical and chemical effects produced by diurnal water fluctuations of the Colorado River on invertebrate fauna at the confluence appear to be substantial. Also, the instability of the substrate contributed to reducing the invertebrate fauna in diversity and productivity.

Fish Fauna

The fish fauna of the Colorado River has been studied mainly in the region known as the Grand Canyon and in Lake Powell and Lake Mead and areas just downstream from Lake Mead (Minckley, 1991b). The Colorado River Basin contains a mixture of native and introduced species. Minckley (1991b) states that although the families and species of fish in the Colorado River are relatively few, over 78% of the species of fish now known from the basin are particular to it. This is a larger percentage of species particular to a given river than is found in any other river in the United States. Because of long-term isolation and its unusual physical characteristics, the Colorado Basin supports one of the most distinctive ichthyofaunas in North America (Minckley, 1991b).

There are several distinctive features about the fish fauna of the Colorado River. The larger fish seem to live longer than in other rivers, and they are more streamlined and fusiform than most fish. Many have small depressed skulls, large predorsal humps or keels, or both, and elongated pencil-thin caudal peduncles may be present. Typically, they have small eyes, expansive and falcated (cycle-shaped) fins, and thick leathery skin. Scales are thin and deeply embedded in the skin and sometimes they almost seem to be absent. These special characteristics seem to be adapted to the severe habitats of the Colorado River. For example, hydrodynamic adaptation such as body and fin shape and the structure and size of the fish help it to maintain a position and maneuver itself in swift turbulent currents. To maintain themselves in the swift currents, large bodies and fins may be necessary. To minimize friction and counteract the abrasive sediments and provide a rigid external sheath to maximize muscle efficiencies, these fish often have small or reduced scales and leathery skin. Small eyes also help to reduce abrasive forces on eye structure. Long life seems to be desirable in this type of environment since the ability to reproduce may span decades rather than years in such an unpredictable habitat. Their large size does not seem adaptive to low discharge.

Most of the species of fish found in the Colorado River were described by 1900. Those collections made by Hubbs and Miller in the late 1930s validate earlier collections. It was quite evident that construction of the Hoover Dam changed the downstream fauna of fish. Some believed that the dams caused the reduction of native fish. Species preferring lentic habitats were introduced into the Colorado River after building of the dams. There was an introduction of bait fish after the dams were built and sport fishing increased (Miller, 1952). By 1960 the native fish population of the lower Colorado had been largely replaced by exotic species, due to the change of habitats and general characteristics of the water. In 1966, the Endangered Species Protection Act, which eventually turned into the Endangered Species Act of 1973, reduced the poisoning and the introduction of undesirable fish.

The National Environmental Protection Act of 1969 recognized that habitats were being lost at an unacceptable rate and mandated assessments and disclosures of impacts of federal projects. Minckley (1991b) lists eight native species of fish in the Grand Canyon National Park, six of which are endemic. The speckled dace and the roundtailed chub are known from adjacent rivers. The humpback chub, bonytail, Colorado spikeminnow, and razorback suckers are listed or proposed as endangered by the Department of Interior (U.S. Fish and Wildlife Service, 1988). Of these species, only the humpback chub has reproductive populations. Other fish are extremely depleted or extirpated. Speckled dace, flannelmouth suckers, and blue suckers remain relatively common (Minckley, 1985).

From Glen and Marble Canyons, 17 species were collected at 27 sites. Most of these were from tributaries. The roundtailed chub, the Colorado spikeminnow; the speckled dace; and flannelmouth, bluehead, and razorback suckers were the native fish that were collected. The nonnative species were the flathead minnow, carp, channel catfish, and green sunfish. The humpback chub was described from three specimens, two from an unknown creek and one from Bright Angel Creek.

Near Lees Ferry the following fish were found: speckled dace, spikeminnow, flannelmouth, bluehead suckers, and nonnative channel catfish in 1934. In Nankoweap Creek dace were caught (Lowe, 1974). A humpback chub was caught in Spencer Creek by Wallace in 1955. After closure of the Glen Canyon Dam, the only large species were the humpback and roundtailed chub, bonytail, and some hybrids (Holden, 1968; Stone and Rathbon, 1967, 1969). Introduced carp, channel catfish, flannelmouth suckers, and bluehead were also there.

The fish fauna is best known between Lees Ferry and Separation Rapids. The species in this reach are the bonytail chub (*Gila elegans* rare), humpback chub (*G. cypha*), the Colorado River chub (*G. robusta*), *Ptychocheilus lucius*, speckled dace (*Rhinichthys osculus*), razorback sucker (*Xyrauchen texanus*), the flannelmouth sucker (*Catostomus latipinnis*), and the bluehead sucker (*Pantosteus* (*Catostomus*) *discobulus*). Introduced species are Coho salmon (*Oncorhynchus kisutch*), rainbow trout (*Salmo gairdneri*), cutthroat trout (*S. clarki*), brown trout (*S. trutta*), brook trout (*Salvelinus fontinalis*), carp (*Cyprinus carpio*), golden shiner (*Notemigonus crysoleucus*), Virgin River spine dace (*Lepidomeda mollispinis*), woodfin (*Plagopterus argentissimus*), red shiner (*Notropis lutrensis*), fathead minnow (*Pimephales promelas*), channel catfish (*Ictalurus punctatus*), black bullhead (*I. melas*), Rio Grande killifish (*Fundulus zebrinus*), striped bass (*Morone saxatilis*), largemouth bass (*Micropterus salmoides*), green sunfish (*Chaenobryttus cyanellus*), bluegill sunfish (*Lepomis macrochirus*), and the walleye (*Stizostedion vitreum*) (Table 1.3).

Twenty-seven fish species are known from the Colorado River in the study area, of which 70% are exotics. In this reach of the Colorado River the fish fauna is composed of species that have been introduced and also a few native species. Several of the native species have become extinct.

Originally in the Colorado River there were eight native species of fish, including the bonytail chub, Colorado (roundtail chub), and Colorado spikeminnow, which are apparently extinct in the Grand Canyon. This disappearance is not restricted to the Grand Canyon area alone since all three have been designated endangered species. Another endangered species native to the Colorado River system is the humpback chub. Populations have been markedly reduced since major habitat changes, although they are still extant in the Grand Canyon area. Recently, it reproduces only near the confluence of the Little Colorado and Colorado Rivers in the canyon. The razorback sucker is thought to be going extinct throughout its former range within the Colorado River basin. It was considered extinct in the Grand

Canyon until three adults were captured near the confluence of the Paria and Colorado Rivers. In the late 1970s and early 1980s, the three native species—the bluehead and flannelmouth suckers and the speckled dace—were represented by what appeared to be healthy reproducing populations through most of their former range. Juvenile suckers remained in the perennial tributaries for two to three years after hatching before moving into the main stream. The speckled dace are found regularly in the tributaries, although their occurrence in the main stream is highly variable.

Nineteen exotic species have been introduced into the Colorado River system. Ten of the 19 exotic species have been observed so infrequently that they should be considered an insignificant component of the Grand Canyon ichthyofauna. Exotic species or introduced species that have been recorded from this area are as follows: golden shiner, green sunfish, bluegill sunfish, Coho salmon, black bullheads, largemouth bass, and red shiner. Largemouth bass and bluegills have occasionally been recorded from the Grand Canyon area. The bass seem to be very localized in occurrence.

The bass was suprisingly the most common species encountered from 237 Mile Rapids to Separation Canyon. However, there are undocumented accounts of striped bass occurring sporadically upstream at Havasu river mile 156.9. Two exotic minnow species that seem to be well established in the Grand Canyon are the fathead minnow and the Rio Grande killifish. They seem to have reached the highest density in the Little Colorado River and Unkar and Kanab Creeks. The four remaining exotic species are trout: rainbow, brown, brook, and cutthroat. All of these have been introduced in sports fishery stocking programs. Rainbow trout is most widely distributed in the area. The brown and brook trout are far less numerous. Cutthroat trout were introduced at Lees Ferry. Capture was in November 1979. It was the most common fish taken by anglers at Badger Rapids.

Although channel catfish are hard to catch, they are probably ubiquitous in the study area. Their density is low above Lava Falls and considerably higher from Lava Falls (between river miles 179 and 180 downstream) with a definite higher concentration occurring between Separation Rapids and the rapids 5 km upstream (between river miles 239 and 240). These fish are fairly common in this reach but are most often found near the confluence of the Little Colorado River. Carp was the most common exotic species found in the Grand Canyon in the collections of Carothers and Minckley.

Twenty-seven species of fish are known to be present or have occurred in the Colorado River and its tributaries in the Grand Canyon reach. The populations of these species are very variable. They rank in abundance in this area as follows: carp, speckled dace, flannelmouth sucker, rainbow trout, bluehead sucker, and humpback chub. Brown and brook trout, fathead minnows, channel catfish, and the Rio Grande killifish are the only other species that appear to maintain stable but low-density populations in the Grand Canyon area.

The juvenile humpback chub forages on or near the substrate, selecting benthic insect larvae and organic detritus as its primary food items. For example, food items identified in the stomach of a single winter mortality consisted of several midge larvae (Chironomidae) and a biting midge larve (Ceratopogonids). Specimens found below Glen Canyon Dam were feeding on planktonic crustacea, which apparently came from Lake Powell. Roundtail chub (*Gila robusta*) is omnivorous, feeding on aquatic and terrestrial insects as well as filamentous algae. *Ptychocheilus lucius*, which is certainly endangered if not extinct in the Grand Canyon, eats primarily larvae, pupae, and nymphs of aquatic insects as well as cladocerans and copepods.

Speckled dace (*Rhinichthys osculus*) feeds on aquatic invertebrates, especially Ephemeroptera, Diptera, and Trichoptera. The blackfly and midge larvae are the most common. Other major food items included mayfly nymphs in winter, seed shrimp (Cypridae) in summer, and net-spinning caddisfly larvae in summer and fall. Larvae of Dobson flies and soldier flies were secondary in importance during the spring. Terrestrial insects were a minor component of the seasonal diets.

In the northern tributaries the speckled dace fed primarily on benthic insects and amorphous organic debris. Adult midges and ants were utilized in small to moderate quantities throughout the year. Other terrestrial insects eaten by the speckled dace included leafhoppers during the winter, a plant hopper, an ichneumonid wasp in the spring, and a ctenuchid moth in the fall. In the southern tributaries the food was similar to that in northern tributaries. Benthic invertebrates predominated in the diet, with blackfly and midge larvae being the most heavily exploited taxa. Other major food items included mayfly nymphs in winter and seed shrimp in summer and net-spinning caddisfly larvae in summer and fall. As in the Grand Canyon area larvae of Dobson flies and soldier flies were of secondary importance in the spring. Terrestrial insects were a minor component of the seasonal diet, with pyralid and ctenuchid moths, adult midges, and ants being the only taxa comprising greater than 0.5% of any seasonal diet. Nonanimal diets included the algae *Nostoc* and detritus. *Nostoc* was eaten primarily through the winter and was limited primarily to speckled dace collected from Hermit Creek.

The razorback sucker is an omnivorous species. The food includes algae and dipteran larvae and may include crustaceans, particularly in the month of May. The flannelmouth sucker is omnivorous and feeds heavily on midges, blackflies, scuds, organic debris, and *Cladophora*. The bluehead sucker (*Catostomus discobolus*) feeds extensively on invertebrates in the study area, their diets consisting primarily of dipterans and scuds. In the main stem of the Colorado River, they fed mostly on blackfly larvae and midge larvae. Other aquatic invertebrates consumed included cranefly larvae in winter and net-winged midge larvae in summer. Adult blackflies and midges were present in small quantities during the summer. Invertebrate gut content included organic debris, which was the principal dietary component during most of the year, and *Cladophora*. Digestive tracts of the bluehead sucker consisted of abundant diatoms of all seasons. Winter samples were dominated by *Diatoma*, *Cymbella*, and *Gomphonema*, whereas *Diatoma*, *Navicula*, *Rhoicosphenia*, and *Cocconeis* predominated during the summer and fall, and in the fall, mainly *Diatoma* and *Cocconeis*.

The main food of rainbow trout (*Salmo gairdneri*) in the main stem of the Colorado were aquatic invertebrates, primarily scuds and blackfly larvae during winter and fall and terrestrial insects in spring and summer. *Cladophora* was an important dietary item throughout the year. Rainbow trout in tributaries utilized benthic invertebrates, *Cladophora*, and to a lesser extent than in the main stem, terrestrial insects. In the main stem the rainbow trout consumed 65 different food items throughout the year. The riverine diet of this species reflects its visual orientation, large body size, and ability to actively exploit food resources throughout its habitat. *Cladophora* constituted from one-fourth to one-half of the dietary intake throughout the year. Based on invertebrate taxa identified from algal masses in the stomach, *Cladophora* was taken from both the substrate and drift. Invertebrates constituted an important element in the annual diet of the main-stem rainbow trout. Aquatic insects dominated the diet in the fall and winter, while terrestrial insects were more heavily utilized in the spring and summer. Scuds comprised the major invertebrate prey of the rainbow trout. Small amounts of midge larvae and pupae were consumed throughout the year. The most heavily exploited terrestrial insects were stinkbugs, grasshoppers, ants, and scarab beetles, which collectively composed a considerable amount of the spring and summer diet.

In the northern tributaries, 61 types of food were ingested by the rainbow trout and the diet was similar to that of the main-stream individuals. *Cladophora* constituted the major portion of the diet in all seasons except summer, when it represented only 8.32% of the stomach contents. Dobson fly larvae appeared to be utilized only in the winter and summer. Individual families of caddisflies were ingested in large quantities whenever present. Net-spinning caddisflies were eaten during the winter and summer, small-case caddisflies (Heliopsychidae) and northern caddisflies (Limnephilidae) in the spring, and fingernet (Philopotamidae) and microcaddisflies in the fall. Collectively, these three families formed from 0.31 to 7.02% of each season's diet. Dipteran pupae were utilized only slightly throughout the year (0.02 to 0.89%), while the larvae, especially of blackflies and midges, were utilized extensively in the summer (25.79%). Scuds were identified in the stomach contents from three of the four sampling periods. Feeding on terrestrial insects was of minor importance in northern tributaries, as terrestrial insects made up only 1.28 to 5.09% of the spring and summer diets, respectively.

Forty-six types of food were identified in the stomachs of rainbow trout taken from southern tributaries. The food was strikingly different in these tributaries from that in the main stream and northern tributaries. *Cladophora* was present in small quantities during fall and winter and absent from the diet in spring and summer. Mayfly nymphs were the major prey item throughout much of the year, ranging from 1.9 to 24.63% of the total diet. Pouch snails (Physidae) were the most common aquatic invertebrate present in the stomach contents during the summer (18.18%) and fall (36.52%). Common Diptera in the diet included blackfly, soldier fly, midge, horsefly, and moth fly larvae, as well as midge and blackfly pupae. Together, these taxa made up 3.48 to 28.29% of the seasonal diet. Dobson fly larvae were heavily preyed upon only in the fall (15.89%). Other aquatic invertebrates consumed in more than trace amounts were predacious diving beetles (Dytiscidae), seed shrimp, net-spinning caddisflies, and scuds. Terrestrial insects, especially grasshoppers, blackflies, and bees, were common prey items in the summer (10.99%) and fall (12.51%).

For brown trout (*Salmo trutta*), scuds and immature dipterans were the major food items throughout the year. However, no specimens were collected in the winter. Several groups, such as pentatomids, ctenuchids, and *Cladophora*, were important seasonally. Aquatic organisms in the stomachs of main-stem river brown trout consisted primarily of scuds, blackfly larvae, and pupae and *Cladophora*. Dominant terrestrial insects in order of importance were stinkbugs, ctenuchid moths, ants, adult blackflies, and grasshoppers. Seasonal variation in brown trout diet were similar to those of rainbow trout. Specimens taken in the spring contain large numbers of *Cladophora*, terrestrial insects, and scuds, which collectively formed 82.3% of the diet. Blackfly larvae and pupae were the primary summer food items and accounted for 64.15% of the total diet. The fall diet consisted primarily of scuds (52.12%), immature blackflies (16.68%), and terrestrial insects (22.24%).

Brook trout (*Salvelinus fontinalis*) feed primarily on larger aquatic invertebrates: scuds, earthworms, and snails. Also present were *Cladophora*, midge pupae, blackfly larvae and pupae, midge larvae, and ants. Adult midges, grass seeds, aphids, and leafhoppers were present in small amounts.

Carp (*Cyprinus carpio*) feeds primarily on *Cladophora* during all seasons. Scuds and midge larvae are the most commonly ingested aquatic invertebrates. They comprise 0.09 to 11.12% of the seasonal diet, the lesser amount in winter and the larger amount in spring. Additional invertebrate prey included aquatic earthworms, blackfly larvae, and midge and blackfly pupae. Few terrestrial insects were ingested. Speckled dace was the only vertebrate found in the carp's stomach. *Cladophora*, which consistently made up the greatest portion of the seasonal diet (55.1 to 86.6%), was most heavily utilized in the summer and fall. Organic detritus and plant seeds were also major dietary items.

The golden shiner (*Notemigonus crysoleucus*) has as its main food blackfly larvae. The Virgin River spine dace (*Lepidomeda mollispinis*) fed primarily on aquatic insect larvae, although algae were also taken when aquatic invertebrates were not present. Woundfin (*Plagopterus argentissimus*), an endangered species, fed primarily on animal matter, although debris, plant material, and algae are also ingested. The red shiner (*Notropis lutrensis*) feeds on plankton, benthic invertebrates, juvenile fish, terrestrial insects, and fish eggs. Fathead minnow (*Pimephales promelus*) fed on dipterans, organic detritus, and small amounts of filamentous algae. Channel catfish (*Ictalurus punctatus*) fed on scuds, immature dipterans, and *Cladophora*. It is truly an omnivore and feeds more on plant material in some of the tributaries. Black bullhead (*I. melas*) is an omnivore, although it becomes carnivorous when animal prey items are abundant. Midge larvae, mayflies, leafhoppers, and organic detritus were the major food items consumed by the Rio Grande killifish (*Fundulus zebrinus*). Flannelmouth bass (*Micropterus salmoides*) feeds largely on small invertebrates, especially zooplankton and aquatic insects. The stomach content of green sunfish (*Lepomis cyanellus*) taken from the main stream during the fall contained primarily blackflies and midges. Unidentified invertebrate remains were a considerable portion of the diet. The food of the young walleye pike (*Stizostedion vitreum*) consists mainly of small crustacea, insects, and fish, while the adults feed mainly on other fish.

STRUCTURE OF AQUATIC COMMUNITIES—EXAMPLE: VASEY'S PARADISE ECOSYSTEM

Vegetative Communities

Vasey's Paradise enters the Colorado River in a reach where riverine conditions exist and the effects of flooding are evident (Figure 1.2). Associated vegetation were the green alga *Pediastrum duplex* var. *clathratum*. In and among the plants were filaments of *Ulothrix* sp. and *Mougeotiopsis* sp.; and the diatom *Cyclotella meneghiniana*, which was probably on the sediment or on the filaments of green algae. Also present was *Melosira varians*, which forms filaments and is probably attached to various plants in the area. Other diatoms present were *Fragilaria vaucheriae*, *Synedra tenera* var. *genuina*, *S. ulna*, and *S. ulna* var. *constricta*. Attached to the algae or other plant material in the area were *Achnanthes affinis*. Widespread were *Achnanthes lanceolata* and *A. lanceolata* var. *dubia*. Also widespread were *A. linearis* forma. *curvata* and *A. linearis* var. *pusilla*. *Achnanthes minutissima* was also very common, as was *Cocconeis pediculus*, which was probably attached to the filamentous algae or other plant stems or leaves that might be present. This was also true for *C. placentula*

Site	River Mile	Site	River Mile
1. Paria River (Lee's Ferry)	0.5	15. Elves Chasm	116.5
2. Vasey's Paradise	31.9	16. Fossil Rapids	125.0
3. Red Wall Cavern	33.0	17. Stone Creek	131.0
4. Showerstall Seep	35.5	18. Tapeats Creek	133.5
5. Nautiloid Seep	36.0	19. Deer Creek	136.3
6. Buck Farm	41.0	20. Kanab Creek	143.5
7. Little Nankoweap Creek	51.5	21. Olo Creek	145.5
8. Little Colorado River	61.5	22. The Ledges	152.0
9. Cardenas Creek	71.0	23. Havasu Creek	156.9
10. Unkar Creek	73.0	24. Prospect Lake	179.0
11. Clear Creek	84.0	25. Pumpkin Springs	212.0
12. Bright Angel Creek	87.9	26. Three Springs Canyon	215.5
13. Crystal Creek	98.5	27. Diamond Creek	226.0
14. Shinumo Creek	108.9	28. Travertine Canyon	229.2

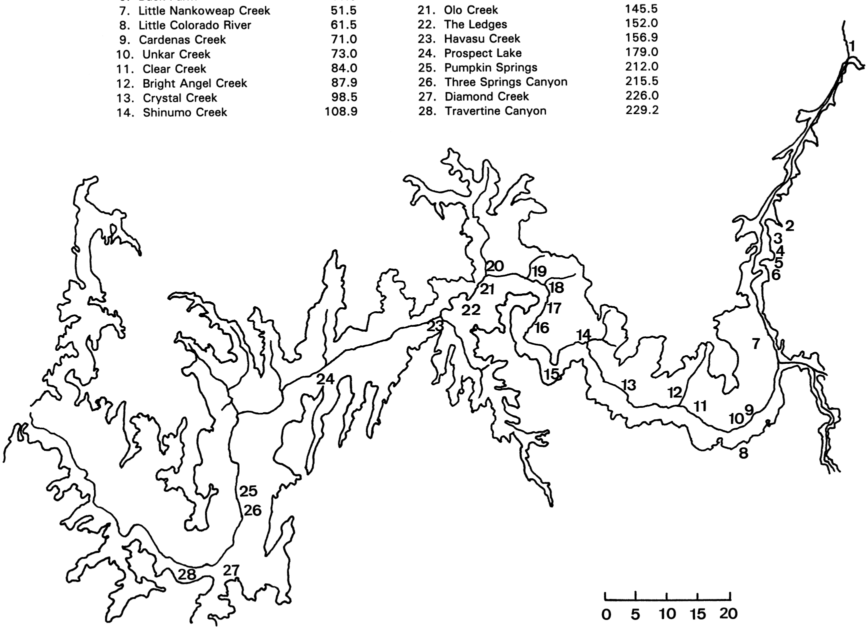

Figure 1.2. Sites sampled along the Colorado River in the Grand Canyon National Park and vicinity. (From Crayton and Sommerfeld, 1978; Stevens, 1983.)

var. *euglypta* and var. *lineata*. The family Cymbellaceae was very common associated with plant material. *Amphora ovalis* var. *pediculus* was widespread, as were *Cymbella affinis* and *C. amphicephala*. Other *Cymbella* species associated with plant debris and with the stems and leaves of plants or the filaments of plants were *Cymbella aspera*, *C. caespitosa* var. *ovata*, *C. hungarica*, and *C. incerta*. Widespread were *Cymbella laevis*, *C. minuta*, and *C. prostrata*. Other common diatoms associated with the vegetation were *Gomphoneis herculeana*, *Gomphonema parvulum*, *G. subclavatum*, and *G. truncatum*. Four taxons belonging to the genus *Diploneis* were also found (Table 1.4) as were three taxons of *Navicula cryptocephala*. These were very common in Vasey's springs. Other *Navicula* species present were *Navicula mutica*, which was widespread; *Navicula mutica* var. *cohnii*; and *N. radiosa*, which was widespread, as was its variety *tenella*. Other widespread *Navicula* species were *N. tripunctata*, *Denticula elegans*, and *D. rainerensis*. Also widespread within the vegetation were *Hantzschia amphioxys* and *Nitzschia apiculata*. Other widespread *Nitzschia* species were *N. dissipata* and *N. frustulum*. Thus the vegetation of both algae and other groups was commonly associated with diatoms.

Several protozoans were found in the habitats associated with the algae. They were an omnivore, *Dinobryon sertularia*, and a protozoan, *Chlamydomonas* sp., which is an omnivore. Other omnivores were the worms *Nais pseudobtusa* and *N. variabilis* and an unidentified species of *Nais*. Gastropods were found associated with plant material in the springs. They were an herbivore–detritivore, *Fossaria obtrussa*; a carnivore, *Physella* sp.; a herbivore–detritivore, *Oxyloma haydeni kanabensis*; and a herbivore–detritivore, *Hawaiia miniscula*. Within the vegetation was found an omnivorous arthropod, *Gammarus lacustris*. Certain chironomids were associated with the debris in Vasey's springs: the omnivorous *Cricotopus annulator* and an unidentified species of *Cricotopus*, which is probably an omnivore. An omnivore–carnivore chironomid, *Eukiefferiella claripennis*, was present, probably feeding on the protozoans and algae and other organisms. Also present was an omnivore–carnivore, *E. coerulescens*. Herbivore–detritivores were also present, as indicated by the occurrence of *Orthocladius luteipes* and *O. rivicola*. Only one fish was reported associated with the vegetation: *Cyprinus carpio*, an omnivore. It is probably an introduced species.

Lentic Communities: Mud and Sand

In muddy sand habitats formed on the bed of the springs were several algae: three taxons belonging to the blue-green algal genus *Oscillatoria*. Also present were three taxons belonging to the genus *Spirulina*. They were found lying on the mud and sand or sandy mud in this habitat. Another species found in this habitat was *Pediastrum duplex* var. *clathratum*. Also present were three taxons belonging to the genus *Scenedesmus*. Another green alga found was a desmid, *Staurastrum* sp.

Several diatoms seemed to prefer this habitat, that is, the mud or sand or muddy sand in this habitat: *Cyclotella meneghiniana* and *Melosira varians*, which were probably attached to or associated with debris in the sandy mud. Also associated with the sandy mud were *Fragilaria construens*; *F. vaucheriae*, which was common; *F. virescens*; and *Synedra acus*, which was probably attached to debris within the sandy mud. Other diatoms present were *Synedra socia*; *S. ulna*, which was widespread; and

(text continues on page 55)

TABLE 1.4. *Species List: Vasey's Paradise in Grand Canyon National Park*

	Substrate[b]				
Taxon[a]	V	M,S	G,R	Source[c]	Feeding Habits[d]
SUPERKINGDOM PROKARYOTAE					
KINGDOM MONERA					
Division Cyanophycota					
Class Cyanophyceae					
Order Chamaesiphonales					
Family Chamaesiphonaceae					
Chamaesiphon incrustans, 1–27				CS	
Order Chroococales					
Family Chroococaceae					
Chroococcus sp., 1–27				CS	
Order Nostocales					
Family Nostocaceae					
Nodularia spumigena, 1–27				CS	
Family Oscillatoriaceae					
Oscillatoria articulata, 1–27		×	×	CS	
O. limosa, 1–27		×	×	CS	
O. nigra, 1–27		×	×	CS	
Spirulina major, 1–27		×	×	CS	
S. subsalsa, 1–27		×	×	CS	
Spirulina sp., 1–27		×	×	CS	
SUPERKINGDOM EUKARYOTAE					
KINGDOM PLANTAE					
Subkingdom Thallobionta					
Division Chlorophycota					
Order Chaetophorales					
Family Chaetophoraceae					
Cloniophora sp., 1–27			×	CS	
Stigeoclonium flagelliferium, 1–27			×	CS	
Stigeoclonium sp., 1–27			×	CS	
Tetraedron sp., 1–27			×	CS	
Family Hydrodictyaceae					
Pediastrum duplex var. *clathratum*, 1–27	×	×		CS	
Family Oocystaceae					
Cerasterias staurastroides, 1–27				CS	
Lagerheimie subsalsa, 1–27				CS	
Family Scenedesmaceae					
Scenedesmus bijuga, 1–27		×		CS	
S. opoliensis, 1–27		×		CS	
S. quadricauda var. *maximus*, 1–27		×		CS	
Order Trentepohliales					
Family Trentepohliaceae					
Leptosira sp., 1–27					
Order Ulotrichales					
Family Microsporaceae					
Microspora floccosa, 1–27			×	CS	
Ulothrix sp., 1–27	×			CS	
Family Monostromataceae					
Gomontia sp., 1–27				CS	
Order Zygnematales					
Family Desmidiaceae					
Staurastrum sp., 1–27		×		CS	

TABLE 1.4. *Continued*

Taxon[a]	Substrate[b] V	Substrate[b] M,S	Substrate[b] G,R	Source[c]	Feeding Habits[d]
Family Zygnemataceae					
Mougeotiopsis sp., 1–27	×		×	CS	
Class Bacillariophyceae					
Order Eupodiscales					
Family Coscinodiscaceae					
Cyclotella meneghiniana, throughout Colorado River	×	×	×	CBT	
Melosira varians, widespread	×	×	×	CBT	
Order Fragilariales					
Family Fragilariaceae					
Asterionella formosa, upper Colorado River			×	CBT	
Diatoma anceps, 1–27			×	CS	
D. elongatum, 1–27			×	CS	
D. hiemale, 1–27			×	CS	
D. hiemale var. *mesodon*, throughout Glen Canyon, especially 18			×	CB	
D. vulgare, widespread			×	CBT	
Fragilaria aequalis, 1–27				CS	
F. brevistriata, 1–27				CS	
F. construens, 1–27		×	×	CS	
F. intermedia, 1–27			×	CS	
F. vaucheriae, widespread	×	×	×	CBT	
F. virescens, 1–27		×		CS	
Synedra acus, common throughout Glen Canyon, abundant 13		×	×	CBT	
S. nana, 1–27		×		CS	
S. socia, widespread, high densities above Little Colorado River		×	×	CBT	
S. tenera var. *genuina*, 1–27	×		×	CS	
S. ulna, widespread	×	×	×	CBT	
S. ulna var. *constricta*, 2	×	×	×	CBT	
Order Achnanthales					
Family Achnanthaceae					
Achnanthes affinis, widespread	×	×	×	CBT	
A. exigua var. *heterovalva*, widespread, especially 2		×	×	CBT	
A. lanceolata, widespread in Glen Canyon	×	×	×		
A. lanceolata var. *dubia*, widespread in Glen Canyon	×	×	×	CBT	
A. linearis f. *curvata*, widespread in Glen Canyon	×	×	×	CBT	
A. linearis var. *pusilla*, widespread in Glen Canyon	×	×	×	CBT	
A. microcephala, widespread in Glen Canyon		×	×	CBT	
A. minutissima, widespread	×	×	×	CBT	
Achnanthidium sp., 1–27				CS	
Cocconeis diminuta, 2, 12, 15, 19			×	CBT	
C. pediculus, widespread	×		×	CBT	
C. placentula var. *euglypta*, widespread	×		×	CBT	
C. placentula var. *lineata*, widespread	×		×	CBT	
Rhoicosphenia curvata, widespread	×		×	CBT	
Order Naviculales					
Family Cymbellaceae					
Amphora ovalis var. *pediculus*, widespread	×		×	CBT	

(continues)

TABLE 1.4. *Continued*

Taxon[a]	Substrate[b] V	Substrate[b] M,S	Substrate[b] G,R	Source[c]	Feeding Habits[d]
Cymbella affinis, widespread	×		×	CBT	
C. amphicephala, widespread	×		×	CBT	
C. aspera, 1–27	×		×	CS	
C. caespitosa var. *ovata*, 1–27	×		×	CS	
C. hungarica, 1–27	×		×	CS	
C. incerta, 1–27	×		×	CS	
C. laevis, widespread in small numbers	×		×	CBT	
C. minuta, widespread	×		×	CBT	
C. prostrata, widespread	×	×		CBT	
C. tumida, widespread		×	×	CBT	
C. turgida, 1–27			×	CS	
C. ventricosa, 1–27		×	×	CS	
C. ventricosa var. *semicircularis*, 1–27		×	×	CS	
Family Gomphonemaceae					
Gomphoneis herculeana, widespread	×			CBT	
G. parvulum, widespread	×			CBT	
G. subclavatum, widespread	×			CBT	
G. truncatum, widespread	×			CBT	
Family Naviculaceae					
Amphipleura pellucida, widespread		×		CBT	
Anomoeoneis exilis, 1–27		×		CS	
A. serians var. *brachysira*, 1–27		×		CS	
A. vitrea, 11, 27		×		CBT	
Caloneis bacillum, widespread		×		CBT	
Diploneis elliptica, 2	×			CBT	
D. oblongella, 2	×			CBT	
D. oculata, 2, 8	×			CBT	
D. puella, widespread	×			CBT	
Frustulia vulgaris, widespread		×	×	CB	
Mastogloia smithii, widespread				CBT	
M. smithii var. *lacustris*, widespread				CBT	
Navicula angelica, 1–27		×		CS	
N. angelica var. *subsalsa*, widespread		×		CBT	
N. arvenensis, widespread		×		CBT	
N. cryptocephala, widespread	×	×	×	CBT	
N. cryptocephala f. *minuta*, widespread	×	×	×	CBT	
N. cryptocephala var. *veneta*, widespread	×	×	×	CBT	
N. decussis, widespread		×	×	CBT	
N. graciliodes, widespread		×		CB	
N. minima, widespread			×	CBT	
N. mutica, widespread	×	×	×	CBT	
N. mutica var. *cohnii*, 2, 15, 18, 27	×	×	×	CBT	
N. pupula var. *rectangularis*, widespread		×		CBT	
N. radiosa, widespread	×	×		CBT	
N. radiosa var. *tenella*, widespread	×	×		CBT	
N. subtilissima, 2, 6		×		CBT	
N. tripunctata, widespread	×		×	CBT	
N. zanoni, widespread, most common in 2, 14, 18				CBT	
Neidium dubium, 1–27		×	×	CS	
Pinnularia sp., 1–27				CS	
Rhopalodia gibba, widespread				CBT	

TABLE 1.4. *Continued*

Taxon[a]	Substrate[b] V	M,S	G,R	Source[c]	Feeding Habits[d]
R. gibberula var. *vanheurckii*, widespread				CBT	
Order Epithemiales					
Family Epithemiaceae					
Denticula elegans, widespread	×		×	CBT	
D. rainerensis, 2, 4, others	×		×	CBT	
Epithemia adnata, 2, 6				CBT	
E. argus var. *alpestris*, 2, 6				CBT	
E. argus var. *longicornis*, widespread				CBT	
E. sorex, widespread				CBT	
E. turgida, upper reaches of Colorado River, below Glen Canyon, but not in Lake Powell area				CBT	
Order Bacillariales					
Family Nitzsciaceae					
Hantzschia amphioxys, widespread	×			CBT	
Nitzschia acicularis, widespread		×		CBT	
N. amphibia, widespread			×	CBT	
N. apiculata, widespread	×			CBT	
N. communis, widespread				CBT	
N. denticula, 2				CBT	
N. dissipata, widespread	×	×	×	CBT	
N. frustulum, widespread	×	×	×	CBT	
N. kutzingiana, widespread			×	CBT	
N. linearis, widespread				CBT	
N. romano, 2, 12, 15		×		CM	
Order Surirellales					
Family Surirellalaceae					
Campylodiscus noricus var. *hibernica*, 2				CBT	
Surirella angustata, widespread		×		CBT	
S. brightwellei, widespread		×		CBT	
Division Chromophycota					
Class Xanthophyceae					
Tetragoniella sp., 1–27				CS	
Order Vaucheriales					
Family Tribonemataceae					
Tribonema utriculosum, 1–27				CS	
Class Dinophyceae					
Order Peridinales					
Family Ceratiaceae					
Ceratium carolinianum, 1–27			×	CS	
C. hirudinella, 1–27			×	CS	
KINGDOM ANIMALIA					
Subkingdom Protozoa					
Class Mastigophora					
Order Cryptomonadida					
Family Cryptomonadidae					
Cryptomonas ovata, 1–27		×		CS	O
Order Chrysomonadida					
Family Ochromonadidae					
Dinobryon sertularia, 1–27	×	×		CS	O
Order Phytomonadida					
Family Carteridae					

(continues)

TABLE 1.4. *Continued*

Taxon[a]	Substrate[b] V	M,S	G,R	Source[c]	Feeding Habits[d]
Carteria klebsii, 1–27				CS	O
Family Chlamydomonidae					
Chlamydomonas sp., 1–27	×	×		CS	O
Family Volvacidae					
Pandorina morum, 1–27		×		CS	O
Order Euglenoidida					
Family Euglenidae					
Colacium sp., 1–27				CS	O
Trachelomonas sp., 1–27				CS	O
Phylum Annelida					
Class Enchytraeidae, 1, 2, 8					
Class Hirudinoidae, 2, 12, 25					
Class Lumbricidae, 2, 12, 25					
Family Lumbriculidae					
Class Oligochaeta					
Order Haplotaxida					
Family Naididae					
Nais pseudobtusa, 2	×	×	×	BSS	O
N. variabilis, 1, 2, 8	×	×	×	BSS	O
Nais sp., 2, 51.6 mi	×	×	×	BSS	O
Family Tubificidae					
Limnodrilus hoffmeisteri, 2, 12; mile 51.6		×		BSS	O
Tubifex tubifex, 1, 2; mile 51.6		×		BSS	O
Phylum Mollusca					
Order Basomatophora					
Class Gastropoda					
Family Lymnaeidae					
Fossaria obtrussa, 1, 2, 8; mile 51.6	×	×		SB	HD
Physella sp., 1–25	×	×	×	SB	C
Family Succineidae					
Oxyloma haydeni kanabensis, 2	×	×		SB	HD
Family Zonitidae					
Hawaiia miniscula, 2	×	×		SB	HD
Order Amphipoda					
Family Gammaridae					
Gammarus lacustris, 1–25	×	×		H	O
Class Insecta					
Order Diptera					
Family Ceratopogonidae					
Family Chironomidae					
Cricotopus annulator, 1–25	×	×	×	BSS	O
Cricotopus sp., 1, 2, 12, 20, 21, 22; mile 51.6	×	×	×	BSS	O
Eukiefferiella claripennis, 1–25	×	×	×	BSS	OC
E. coerulescens, 1–12	×	×	×	BSS	OC
Orthocladius luteipes, 2	×	×	×	BSS	HD
O. rivicola, 1–25	×	×	×	BSS	HD
Parakiefferiella sp., 2, 12, 20	×	×	×	BSS	O
Pseudosmitta sp., 2			×	BSS	O
Family Simuliidae					
Simulium arcticum, 1–25			×	BSS	O

TABLE 1.4. *Continued*

	Substrate[b]				
Taxon[a]	V	M,S	G,R	Source[c]	Feeding Habits[d]
Phylum Chordata					
Subphylum Vertebrata					
Class Osteichthyes					
Order Cypiniformes					
Family Catostomidae					
Catostomus latipinnis, widespread		×	×	CBT	O
Pantosteus (*Catostomus*) *discobolus*, widespread		×	×	CBT	O
Order Cypriniformes					
Family Cyprinidae					
**Cyprinis carpio*, widespread	×	×		CBT	O
**Pimephales promelas*, widespread		×		CBT	O
Rhinichthys osculus, widespread		×		CBT	O
Order Salmoniformes					
Family Salmonidae					
**Salmo gairdneri*, widespread			×	CBT	C
**S. trutta*, widespread			×	CBT	C
**Salvelinus fontinalis*, widespread			×	CBT	C

[a]An asterisk indicates an introduced species. Numbers indicate the sites where the samples were collected.
[b]V, vegetation and debris; M, mud; S, sand; G, gravel; R, rubble.
[c]BSS, Blinn et al. (1992); CB, Czarnecki and Blinn (1978); CBT, Czarnecki et al. (1976); CM, Carothers and Minckley (1981b); CS, Crayton and Sommerfeld (1978); H, Haury (1986); PP, Polhemus and Polhemus (1976); SB, Spamer and Bogan (1993).
[d]Feeding habits: C = carnivore; HD = herbivore-detritivore; O = omnivore; OC = omnivore-carnivore.

S. ulna var. *constricta*, which was present. Probably attached to sand or muddy particles were eight taxons belonging to the genus *Achnanthes*. These were widespread in this habitat (Table 1.4). Several *Cymbella* species were found associated with the mud and sand: *Cymbella prostrata* and *C. tumida*, which were common. Also present were *C. ventricosa* and *C. ventricosa* var. *semicircularis*. In quiet areas associated with the fine mud were the diatoms *Amphipleura pellucida*, *Anomoeoneis exilis*, *A. serians* var. *brachysira*, *A. vitrea*, and *Caloneis bacillum*. *Frustulia vulgaris* was also present associated with the mud and plant debris. Also in this habitat were *Navicula angelica*; *N. angelica* var. *subsalsa*, which was widespread; *N. arvenensis*; *N. cryptocephala*; *N. cryptocephala* forma. *minuta*; *N. cryptocephala* var. *veneta*; *N. decussis*; and *N. graciliodes*. All of these were very common in this habitat, that is, associated with fine sand and mud and organic debris. Other *Navicula* species common in this habitat were *N. mutica*; *N. mutica* var. *cohnii*; *N. pupula var. rectangularis*; *N. radiosa*, which was widespread; and *N. radiosa* var. *tenella*, also widespread. Other *Navicula* species were *N. subtilissima* and *Neidium dubium*. The family Nitzschiaceae, which is often associated with debris and mud, was represented by *Nitzschia acicularis*, *N. dissipata*, *N. frustulum*, and *N. romano*, and two species of *Surirella*, *Surirella angustata* and *S. brightwellei*.

Various protozoans were found associated with the fine mud and debris. They were the omnivores *Cryptomonas ovata*, *Dinobryon sertularia*, *Chlamydomonas* sp., and *Pandorina morum*. They consume plant material as well as very small protozoans and invertebrates.

Worms present in this habitat were *Nais pseudodobtusa, N. variabilis*, and an undescribed species of *Nais*. Tubificid worms in this habitat were the omnivorous *Limnodrilus hoffmeisteri* and *Tubifex tubifex*. A few molluscs were found in this habitat: a herbivore–detritivore, *Fossaria obtrussa*; a carnivore, *Physella*; and the herbivore–detritivores *Oxyloma haydeni kanabensis* and *Hawaiia miniscula*. Also present was an amphipod, *Gammarus lacustris* (Table 1.4).

Several Chironomidae were present in this habitat, which consisted of fine mud, muddy sand, and organic debris, particularly plant debris. They were *Cricotopus annulator*, an omnivore; and an unidentified species of the same genus. The omnivore–carnivores *Eukiefferiella claripennis* and *E. coerulescens* were common, as were the herbivore–detritivores *Orthocladius luteipes* and *O. rivicola*. Another omnivore present was an unidentified species of *Parakiefferiella* sp.; most species of this genus identified are omnivorous.

Several fish were found in this habitat, probably in pools associated with the fine mud and sand. They were the omnivorous *Catostomus latipinnis*, which was widespread; and the omnivorous *Pantosteus* (*Catostomus discobolus*). Several cyprinids were also found: *Cyprinus carpio*, which was widespread; *Pimephales promelas*, an omnivore also introduced; and the widespread but probably native omnivore *Rhinichthys osculus*.

Lotic Communities: Vegetation, Rocks, Gravel, and Coarse Sand

Mainly vegetation, but also rocks, gravel, and coarse sand formed excellent habitats for many species in Vasey's Paradise. On the gravel, intermixed with mud, were found *Oscillatoria articulata, O. limosa, O. nigra, Spirulina major, S. subsalsa*, and *Spirulina* sp. These blue-green algae were fairly common and probably result from use of this area for various human expeditions. Green algae, fairly common, were the pollution-tolerant species of *Stigeoclonium flagelliferium* and an unidentified species of *Stigeoclonium*. Also present was an unidentified species of *Cloniophora*. Present were colonies of *Tetraedron* sp. Blue-green algae present in this habitat were *Microspora floccosa* and *Mougeotiopsis* sp.

The diatoms *Cyclotella meneghiniana* and *Melosira varians* were quite common. Other species found in this habitat, which may have been growing there or perhaps were deposited there, were *Asterionella formosa, Diatoma anceps, D. elongatum, D. hiemale*, and *D. hiemale* var. *mesodon*, and common everywhere was *D. vulgare*. Also in this habitat were found *Fragilaria construens, F. intermedia*, and *F. vaucheriae*, which was attached to the rocks or to gravel or debris in this habitat. Present on the surface of the substrate, that is, gravel and sand, was *Synedra acus*, which was very common. Also present were *S. nana, S. socia* (in the Little Colorado River, which entered this habitat), and *S. tenera* var. *genuina*. *Synedra ulna* was widespread and present was *S. ulna* var. *constricta*. Attached to the gravel and rocks in places where the current was not very strong were *Achnanthes affinis, A. exigua* var. *heterovalva, A. lanceolata, A. lanceolata* var. *dubia, A. linearis* forma. *curvata*, and *A. linearis* var. *pusilla*. Also common in this habitat were *A. microcephala* and *A. minutissima*.

Attached to the rocks were also found *Cocconeis diminuta*, *C. pediculus*, *C. placentula* var. *euglypta*, and *C. placentula* var. *lineata*. Also common in this habitat was *Rhoicosphenia curvata*. Attached to the rocks and gravel were several taxons belonging to the family Cymbellaceae. They are food organisms for many types of aquatic invertebrates. The species present were *Amphora ovalis* var. *pediculus*, *Cymbella affinis*, and *C. amphicephala*. These three taxons were very common. Other members of the Cymbellaceae were found attached not only to rocks and gravel but also to filaments of algae or moss that lived in these habitats, where the flow was relatively rapid. They were, as seen in Table 1.4, 10 more taxons belonging to the genus *Cymbella*.

Also associated with the habitat where the flow was relatively rapid and rocks and gravel were the common substrates was *Frustulia vulgaris*. It probably occurred in areas between rocks or behind rocks where the flow was relatively slow. Widespread in this habitat were *Navicula cryptocephala*, *N. cryptocephala* forma. *minuta*, and *N. cryptocephala* var. *veneta*. Other common *Navicula* species were *Navicula decussis* and *N. minima*. Also common was *Navicula mutica*. Present in this habitat where the current was relatively swift was *N. mutica* var. *cohnii*. In among the rocks where the current was probably moderate were *N. tripunctata* and *Neidium dubium*. Also widespread in this habitat, where a current was present, were *Denticula elegans* and *D. rainerensis*. In among the rocks where the current was probably moderate were *Nitzschia amphibia,* which was widespread. Other common *Nitzschia* species were *N. dissipata*, *N. frustulum*, and *N. kutzingiana*.

Two species belonging to the family Ceratiaceae which are Dinophyceae were *Ceratium carolinianum* and *C. hirudinella*. Within the gravel were three worms believed to be omnivores. They belonged to the genus *Nais* and were *N. pseudobtusa*, *N. variabilis*, and an unidentified species of *Nais*. A single snail was found in this habitat, and it is believed to be a carnivore. It is an unidentified species of the genus *Physella*. In this habitat where the water was moving fairly rapidly but algae and other debris were present in among the rocks were found a number of chironomids. They were the omnivorous *Cricotopus annulator* and an unidentified species of the same genus. Also present were the omnivore–carnivores, *Eukiefferiella claripennis* and *E. coerulescens*. Two herbivore–detritivore taxons were also present: *Orthocladius luteipes* and *O. rivicola*. Other omnivores present were an unidentified species of *Parakiefferiella*, *Pseudosmitta* (an unidentified species), and the omnivorous *Simulium arcticum*.

Several species of fish were found in areas where the flow was fairly rapid: the omnivorous *Catostomus latipinnis* and *Pantosteus (Catostomus) discobolus*. They were widespread wherever the current was fairly rapid. A few species belonging to the family Salmonidae were there: *Salmo gairdneri, S. trutta*, and *Salvelinus fontinalis*. They are all carnivores believed to be introduced species.

SUMMARY

The Colorado River, which is 1360 miles (2190 km) in length, begins its long journey to the Gulf of California in Grand County, Colorado on the Continental Divide. It is formed by many small streams that receive their water from snow melting in the high Rocky Mountains. Downstream the Colorado is joined by the Gunnison, which is formed by the North and South Branches. The Uncompahgre River then joins the Colorado. Farther downstream the San Miguel and Dolores Rivers join the Colorado in northern Utah. The Green River, which is the longest tributary of the Colorado, joins it in Utah. The Green River rises in the Wind River Mountains of Wyoming. The Green River is joined by the Little Snake and the Yampa and White Rivers. Farther downstream the Green River is joined by the Duchesne, Price, San Rafael, and Dirty Devil Rivers. The Moab Canyon of Utah intersects with the Green River. Below the junction of the Green and Colorado Rivers is the Escalante River, which ends in the mouth of Lake Powell. The San Juan joins the Colorado in the region of Lake Powell. It is the largest river to join the Colorado. The San Juan is not only Colorado's largest river but also the largest river in New Mexico. The headwaters of the San Juan are in southwestern Colorado near Wolf Creek Pass. The San Juan receives not only many streams from Colorado but also streams that join it from New Mexico. Paria River joins the Colorado from 200 miles (321.87 km) south of the junction of the Colorado and the San Juan. Pipe Creek enters the Colorado River between river miles 88 and 89.

The vegetation along the Colorado River is sparse and consists of seep willow, Bermuda grass (*Cynodon dactylon*), and scratch grass. Hermit Creek enters the Colorado River from the south at river mile 95. Crystal Creek enters the river from the north rim between river miles 98 and 99. The Shinumo Creek enters the Colorado River from the northwest between river miles 108 and 109. The water temperature of Shinumo Creek at its mouth was 6 to 20°C when this study was made. However, the temperature of the water at the base of the waterfall was 10.5°C. Elves Chasm is located between river miles 116 and 117, where Royal Arch Creek enters the Colorado River.

Stone Creek enters the Colorado River from the north rim between river miles 131 and 132. It is an intermittent stream. Tapeats Creek enters the Colorado River near the north rim between river miles 133 and 134. Tapeats Creek contributes the largest discharge into the Colorado River from the north side of the Grand Canyon. Deer Creek enters the Colorado River from the north bank between river miles 136 and 137. Kanab Creek enters the Colorado River in Arizona between river miles 143 and 144. Kanab Creek is a sulfate stream low in nitrogen and phosphorus and relatively high in silica. 150 Mile Canyon, a small stream, flows intermittently into the Grand Canyon area between river miles 149 and 150. Near the mouth of the creek are small pools surrounded by seep willow, sawgrass, bullrush, and scratch grass. Above the falls of this creek, bullrushes, scratch grass, blue-eyed grass, and maidenhair fern line the canyon walls.

Havasu Creek enters the Colorado River from the south side of the canyon between river miles 156 and 157. This creek's water is dominated by calcium and magnesium carbonates and has a silicate concentration second only to that in Diamond Creek. Nitrogen and phosphorus values are low in Havasu Creek. Specific conductance is 660 to 740 $\mu S\ cm^{-1}$. The pH ranges from 8.3 to 9.0. National Canyon enters the Colorado River from the southeast between river miles 166 and 167.

Three Spring Canyon enters the Colorado River between river miles 215 and 216. It is an intermittent creek. The stream 217 Mile Canyon enters the canyon between river miles 217 and 218.

Diamond Creek enters the Colorado River from the north between river miles 225 and 226. At its mouth it is wide with little vegetation. Seep willow, cattails, and rabbit foot grass occur at or near the margins of the stream. The water temperature at the mouth ranges from 12° to 27°C. An intermittent stream, Bridge Canyon, enters the river between river miles 235 and 236.

Above Hoover Dam at Grand Wash (river mile 276), the river turns sharply right and flows south again, forming the boundary between Arizona and Nevada. In this area it is joined by the Virgin River from the Zion Canyon and the Bill Williams River, which drains 5400 m^2 in Arizona. Near Yuma, the Colorado receives the Gila River, which rises in the Elk Mountains. It is 1010 km long and one of the most important rivers in America's Southwest. Coolidge Dam was constructed on the Gila River in 1928. Its reservoir holds about 6000 million feet of water. The Gila is Arizona's largest river and drains approximately 56,000 square miles. Downstream from Hoover Dam is Davis Dam. The Colorado downstream forms the boundaries between California and Arizona. The next humanmade impediment is Parker Dam at the southeastern end of Lake Havasu. Parker Dam is the beginning of the Colorado Aqueduct, which carries the water to the city of Los Angeles and other areas of southern California. Besides the large reservoirs mentioned above, the Imperial and Leguna Reservoirs, which are largely for irrigation, are formed on the Colorado River. In Mexico, the Colorado flows between the area known as the Sonora and the mainland from the upper district of the penninsula of lower California. Hence it moves slowly into the Gulf of California and sinks its red waters into the blue waters of the ocean.

The Colorado River has three distinct sections: the Upper Basin, the plateau section, and the Lower Basin. Many dams have been built on the Colorado River system. The major dams on the Colorado proper are the Glen Canyon Dam and Hoover Dam. Smaller dams are also located on the Colorado River. The geology of the Colorado River basin is highly varied and is composed of igneous, metamorphic, and sedimentary rock types as well as clays. The soils of the basin resemble the geological formations from which they are derived. The geology of the Grand Canyon is highly varied in the types of rocks and sands that it contains.

The biology of the watershed of the Colorado River is best known between the Glen Canyon and Hoover Dams. Woody species of the riparian area contribute greatly to the support of the insects and other invertebrates present because this area is less subject to floods and droughts. The present native species are a minor component of the overall flora because of introduced species. There is an ever-increasing predominance of salt cedar, camelthorn, and herbaceous species such as yellow clover and spiny sow thistle. A nonnative plant along the river is tamarisk, commonly known as salt cedar. The salt cedar is a poor habitat for most wildlife except for the mourning dove and the white-winged dove. The salt cedar attracts insects as well as riparian birds. Another plant of import is the camelthorn, a spiny leguminous half-shrub that has invaded several beaches, especially in the upper portion of the canyon. The Russian olive is also fairly common in the canyon. It attracts the mourning dove as well as other bird species. Other species important to wildlife are the western honey mosquite, the catclaw acacia, and the coyote or sandbar willow. Seep willows are represented by two species: *Baccharis saliscifolia* is common along the river and *B. emoryii* along the sidestreams. The herbaceous riparian species are foxtail broom and Bermuda grass, as well as several other plants that have been discovered in this reach: that is, the Grand Canyon reach.

The amphibians in the Colorado River are usually associated with moist habitats: one species of salamander and five species of toads and frogs, four of which were found. Grand Canyon rattlesnake or pink rattlesnake occurs frequently in riparian habitats of the Colorado River. Seven species of lizards are found in the riparian zone. Because of greater vegetation biomass, the reptile population has been increased since the river flow has been stabilized. An increase in insects has also occurred. In 1978, 284 species of birds were known from the Grand Canyon. Most of the species of birds that are found are insectivorous, and therefore the relatively high insect populations and low human populations probably account for their being present. Seventy-eight species of birds have been reported by Hoffmeister (1971). Forty of these occurred in the inner gorge, and most of these occurred in the riparian zone. Two endangered bird species of the riparian zone are the bald eagle and the peregrine falcon. The mammals are restricted to riparian mammals such as beavers, or to a lesser amount to bighorn sheep.

Dam-related effects such as clarity, pattern of flow, and water temperature override the geomorphological influences on habitat availability. The recovery of the benthos did not seem to be correlated with the abundance of the fish but rather with the geomorphological differences in substrate availability between reaches, mediated by dam and tributary effects on water clarity and the amount of the benthos. Reaction between flow regulation and geomorphology produced a pattern of circuitous recovery of some physical river systems characteristic of distance from the dam. Improving discharge management for endangered native fish species requires detailed understanding of the existing and potential benthic development and trophic interactions. Many factors are involved in recovery of the benthos and hence the fish populations.

Vegetation is necessary for mammals, and mammals have a profound effect on the existing vegetation. For example, severe damage to vegetation may be created by foraging and trampling. This is particularly true of feral animals. The lack of establishment of Goodding willows and Fremont cottonwoods is probably due to beavers. Seedling establishment is not well understood for most woody riparian species. Grand Canyon species are short on endemics and rare species. Two previously undescribed species of flowering plants, *Flaveria mcdougalii* and *Euphorbia aaron-rossii*, are such plants. The riparian vegetation of the Grand Canyon is very important to the aquatic life of the river. It is the high diversity of the aquatic life that supports the high diversity of birds and amphibia, and the aquatic insects are very important to the fish.

Associations of Aquatic Organisms: Glen Canyon Dam to Hoover Dam. This reach of the river is often known as the Grand Canyon reach. The algae are sometimes free-floating and seem to be part of the attached vegetation, which has been broken off by flow. The algae may be found on fine sediments in backwaters within submerged vegetation. The areas of algae attachment were the scoured rock faces in areas of rapids and cataracts and fine sediments in backwaters, usually along the inner side of river bends. Various submerged macrophytes also serve as habitats for algae such as diatoms. Many of the plankton species are believed to be detached from various surfaces. The biodensity of diatom species of the Colorado River after impoundment was 1600-fold lower than the cell density prior to impoundment of the river.

Crayton and Sommerfeld (1978) reported 127 species of phytoplankton in the Colorado River. Many of these were detached and dislodged from substrates. The dominant species of diatoms were *Diatoma vulgare*, *Rhoicosphenia curvata*, and *Cocconeis pediculus*. Many of these algae are known to have been detached forms from substrates in Lake Powell.

Cladophora glomerata is the dominant attached filamentous green algae in the canyon, especially between Glen Canyon Dam and Paria River and at the mouths of tributaries. This algae was also the dominant algae for sites at and above Lees Ferry. A relatively high amount of biomass of *Cladophora glomerata* in upstream tailwater sites may be the result of stable rock faces for attachment and nutrient-enriched waters. Abrupt drops in *Cladophora* at Lees Ferry were probably due to episodes of desiccation and reduced input of nutrients. *Cladophora* seems to thrive under continuously submerged clear-water habitats. *Cladophora glomerata* seems to prefer shallow waters and decreases with greater depth, probably due to rapid attenuation of light caused by periodically high sediment loads. There seemed to be some correlation in *Cladophora glomerata* with channel depth at sites above Lees Ferry. Similarly, there was a decrease in biomass with depth at sites below Lees Ferry.

Cladophora glomerata was found to be a habitat for the amphipod *Gammarus lacustris* and other snails and invertebrates. It also provides a large amount of surface for the attachment of epiphytic diatoms, which are an important food source for aquatic invertebrates and, in some cases, for fish.

The diatoms were the dominant form of algae, followed by cyanobacteria and chlorophytes. At the confluence of Diamond Creek, a red alga, *Batrachospermum* sp., was reported, and *Audouienella* sp. was found attached to filaments of *Cladophora*. The dominant diatom taxa were *Diatoma vulgare*, *Synedra ulna*, and *Cocconeis pediculus*. *Achnanthes affinis*, *Cocconeis pediculus*, *Diatoma vulgare*, and *Rhoicosphenia curvata* made up 80% of the communities upstream from Lees Ferry. However, these four taxa were less important at downstream sites, and *Gomphonema olivaceum*, *Cymbella affinis*, and *Nitzschia dissipata* became more important at the downstream sites. It is believed that the change in species composition was due to their tolerance to suspended sediments.

Below Lees Ferry there was a fourfold decrease in epiphytic diatoms. It is difficult to compare the aquatic invertebrates before and after dam closure because of the introduction of many individuals of insects, snails, and leeches. The zooplankton and the algae seemed to be derived from lentic populations in Lake Powell. There seemed to be some correlation with the increase in populations of *Cladocera* and copepods with the temporary rise in water due to patterns of releases from the dam. Below the dam, the microcrustacea also increased. A large percent of the copepod planktors were in poor condition and increase downstream.

Of the 34 invertebrates listed by Haury (1986) only 16 were true planktors. Others were the benthic species. These species, which have broken loose and drifted downstream, contributed most of the biomass. Other planktors listed by Kubly are rotifers (*Collembolan*) and water mites. The last two are characterized best as epineustonic. The mites are probably nectonic.

Backwaters and borders of the rivers appeared to be refugia for some invertebrates. There seemed to be a higher productivity of these invertebrates in the backwaters. Most of the sites for aquatic life are located near the mouths of tributaries and around debris caught in the river in the Grand Canyon National Park and vicinity. Just below Glen Canyon Dam, the current is stochastic and the water is generally clear and deep. The rapid flow inhibits many different types of organisms.

The habitats for algae consisted mainly of other algae, submerged leaves, and stems of vascular plants. Some mosses also were habitats of algae. A green alga, *Cladophora glomerata*, is much more prevalent than it was in the early days of the Colorado River and seems to have been increased because of the dams, resulting in clearer water with increased light penetration and greater stability of the riverbed.

Seasonal extremes in discharged sediment loads and temperature seemed to have been eliminated since the construction of Grand Canyon Dam. The discharge is now regulated by power demands. The maximum is about 566 cm s^{-1} and the daily minimum is 130 cm/s^{-1}, with extremes ranging from 28 to 764 cm/s^{-1}. Water entering the river below the dam is cold and clear. The temperature ranges from 15 to 60°C.

Invertebrates in the main stem of the Colorado River are generally low in productivity, except in the section between Glen Canyon Dam and the confluence of the Little Colorado River, where the sediment input was minimum. Here the estimates of density were several thousand individuals per square meter. In contrast, grabs taken below the confluence of the Little Colorado River usually yielded only 5 to 10 individuals per square meter. These were blackflies, midges, and aquatic earthworms, which were collected on exposed gravel in the stream channel and along the margins of the river. The density of invertebrates seemed to be lower at the confluence of tributaries. Insects are fewer in spring and summer. The productivity in the main stem of the Colorado River seemed to be lower than in the tributaries and other riverine systems. This seems to be caused by the cooler annual temperature, the greater depth, the current velocity, and sediment input. Common invertebrates in the main stream were freshwater amphipods and aquatic earthworms.

The diversity of insects seemed to be lower than expected, probably because high canyon walls to the north and south, combined with the topographic variability created a formidable dispersal barrier for aquatic species. Canyon topography has effectively blocked northern dispersal of some species. Spring and summer productivity and diversity were lowest. It is probably due to spring runoff and summer flash floods from the tributaries that disrupt the benthic invertebrate communities. The small amount of flooding in fall and winter favored algae and invertebrate productivity. The main stream of the Colorado River is typically cooler than the tributaries.

This may have greatly influenced the invertebrate fauna. Furthermore, turbidity and suspended solids were higher in the main stream than in the tributaries. It is undoubtedly a combination of unstable physical and chemical parameters that reduces the fauna in the mouths of the tributaries and in the Colorado River just below the entrances of tributaries. In general, the productivity of invertebrates was lower in the main channel than in the tributaries. This is due to the river's cooler annual temperature, greater depth, current velocity, and sediment input.

The areas that produce the richest invertebrate fauna are shallow backwaters and eddies along the margin of the river. The influence of physical and chemical effects produced by the diurnal water fluctuations of the Colorado River on the invertebrate fauna at the confluences appears to be substantial. The instability of the substrates also contributes to reducing the invertebrate fauna in diversity and productivity.

The fish fauna of the Colorado River has been studied primarily in the region of the Grand Canyon and in Lake Powell and Lake Mead. The Colorado River Basin contains a mixture of native and introduced species. Over 78% of the species of fish now known from the basin are particular to it. This is a larger percentage of species particular to a given river than that found in any other river in the United States. This is probably because of its long-term isolation and its unusual physical characteristics. There are several distinctive features about the fish fauna of the Colorado River. The larger fish seem to live longer than in other rivers, and they are more streamlined and fusiform than most fish. Many have small depressed skulls, large predorsal humps or keels or both, and elongated pencil-thin caudal peduncles. Typically, they have small eyes, expansive and falcated fins, and thick leathery skin. Scales are thin and deeply embedded in the skin, and sometimes they almost seem to be absent. These special characteristics seem to be adapted to the severe habitats of the Colorado River. These characteristics seem to be important in allowing the fish to maintain position and maneuver itself in swift turbulent currents. The small eyes help to reduce the erosive forces on the eye.

In 1960, the native fish populations of the lower Colorado had been largely replaced by exotic species due to changes of habitat and general characteristics of the water. The humpback chub, bonytail, Colorado spikeminnow, and razorback suckers are listed or proposed as endangered by the Department of Interior (U.S. Fish and Wildlife Service, 1988). Of these species only the humpback chub has reproductive populations. Other fish are extremely extirpated. Speckled dace, flannelmouth suckers, and blue suckers remain relatively common. The fish fauna is best known between Lees Ferry and Separation Rapids. Twenty-seven fish species are known from the study area, of which 70% are exotics. Originally in the Colorado River there were eight native species of fish, including the bonytail chub, Colorado roundtailed chub, and Colorado spikeminnow, which are apparently extinct in the Grand Canyon. Humpback chub is also endangered. The razorback sucker is thought to be going extinct.

Although 19 exotic species have been introduced into the Colorado River, 10 of the 19 have been observed so infrequently that they should be considered as an insignificant component of the Grand Canyon ichthyofauna. Exotic minnow species that seem to be well established in the Grand Canyon are the fathead minnow and the

Rio Grande killifish. Species of trout have been introduced by the sports fisheries stocking programs. Rainbow trout is most widely distributed in the area. The brown and brook trout are far less numerous. Cutthroat trout were introduced at Lees Ferry. In November 1979 it was the most common fish taken by anglers at Badger Rapids.

Channel catfish are probably ubiquitous throughout the study area, although they are hard to catch. Twenty-seven species of fish are known to be present or have occurred in the Colorado River and its tributaries in the Grand Canyon reach.

The fish fauna is well sorted as to its feeding habits. Some feed largely on algae, whereas others feed on a variety of invertebrates, insects, and even small fish. Besides aquatic insects, the fish fauna feed upon terrestrial insects. The most heavily exploited are stinkbugs, grasshoppers, ants, and scarab beetles. Thirty-six types of food have been identified in the stomach of the rainbow trout taken in the southern tributaries. The food was strikingly different in these tributaries from that of the main stream and northern tributaries. *Cladophora* was present in small quantities during fall and winter and absent from the diet in spring and summer. Mayflies were the major prey. Pouch snails were the most common aquatic invertebrate present in the stomach contents during the summer. Common Diptera in the diet included blackfly, soldier fly, midge, horsefly, and moth fly larvae, as well as midge and blackfly pupae. Other aquatic invertebrates consumed were diving beetles, sea shrimp, net-spinning caddis, and scuds. Of the terrestrial insects, grasshoppers, blackflies, and bees were common prey, particularly in the summer and fall. Most of the fish fed on a variety of foods, particularly insects. However, the carp feed primarily on *Cladophora* during all seasons. Scuds and midge larvae are the most commonly ingested aquatic invertebrates, but they form less than 12% of the seasonal diet. The fish fauna consists of a variety of species feeding on different forms of aquatic life, particularly insects, and in some cases, a fair amount of algae was consumed.

The structure of the aquatic communities is described for Vasey's Paradise ecosystem as an example. The basic structure of the ecosystems in these various habitats is based on algae. Protozoans and small invertebrates are detritivores, herbivores or omnivores. Larger invertebrates and a few fish are omnivores or carnivores. In other words, the ecosystem consisting of four stages of nutrient and energy transfer is well exemplified in Vasey's Paradise, which illustrates the general ecosystems in the Grand Canyon reach.

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