INLAND FISHES of CALIFORNIA

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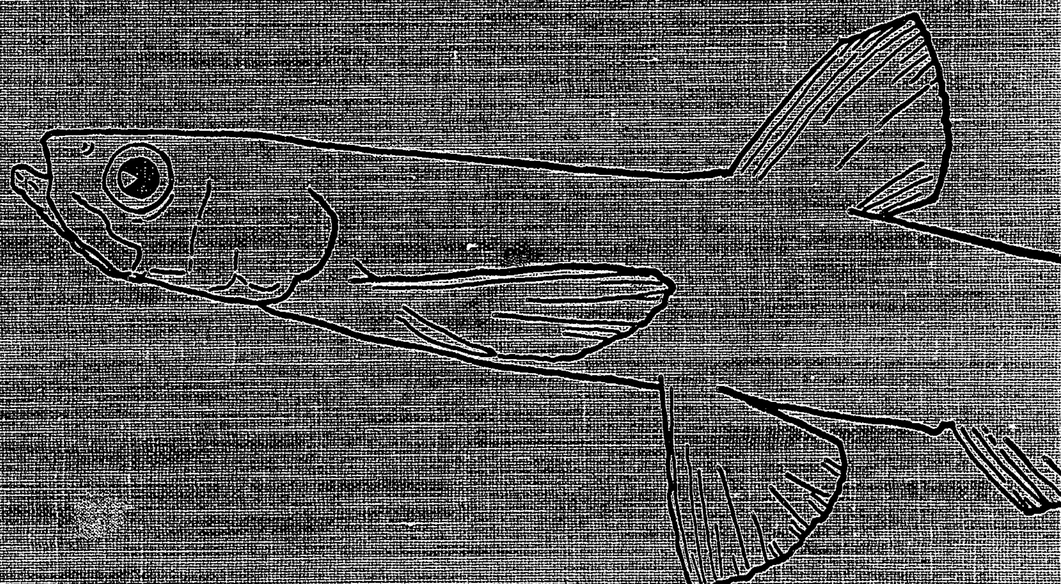

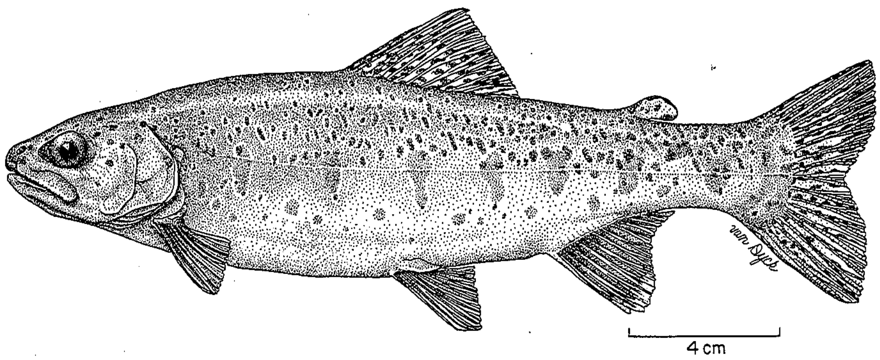

Figure 39. Rainbow trout, 21 cm SL, California.

Rainbow Trout, *Salmo gairdneri* Richardson

Systematic Note. Rainbow trout are the most abundant and widespread species of western *Salmo*. They are successful because they have been able to adapt to a wide variety of aquatic habitats (including fish hatcheries) and are flexible in their life-history patterns. As a result, many local populations of rainbow trout have distinctive characteristics, and have been given separate common and scientific names. Within these populations, however, variation is often considerable. Distinctive characteristics, especially color patterns, are often at least in part phenotypic responses to local conditions and may be lost is the fish are transferred to a hatchery or to another stream (Needham and Gard, 1959). The widespread mixing of rainbow trout from different populations by man, in hatcheries and through indiscriminate planting, has further blurred the distinctions between populations, especially in California. Thus, the six subspecies of rainbow trout in California that have been officially recognized by the California Department of Fish and Game (McAfee, 1966) are all of questionable validity.

The steelhead rainbow trout, *S. g. gairdneri*, is the anadromous form. Aside from their sea-going habits and large size at spawning there is little to distinguish them from rainbow trout that are resident in the same streams that steelhead use for spawning.

The Kamloops rainbow, *S. g. kamloops*, is a hatchery strain derived from trout native to Kamloops Lake, British Columbia, and planted mostly in large California reservoirs (e.g., Shasta Lake). The lack of truly distinctive characteristics in the original Kamloops rainbow trout (McPhail and Lindsey, 1970), together with changes in their genotype in California created by selection in hatcheries and interbreeding in the wild with other varieties, leaves little reason to continue to recognize the Kamloops trout as a subspecies. However, there may be some utility in continuing to recognize it as a lake-adapted hatchery strain (but without the formal trinomial nomenclature).

The Shasta rainbow trout, *S. g. stonei*, from the McCloud River, was the original California rainbow selected for hatchery culture (Wales, 1939). Widespread planting of derivatives of this form over California (and over the world) combined with hatchery selection pressures and hybridization with other forms have largely eliminated whatever distinctive traits they may once have had. Also, the original description may have been based on steelhead rainbow trout. It should be noted, however, that brilliantly colored populations of rainbow trout still live in the McCloud River. Their systematic position is worth investigating.

The Kern River rainbow trout, *S. g. gilberti*, is (or was) a distinctive, heavily spotted form from the upper Kern River. Schreck and Behnke (1971), however, consider it to be a subspecies of golden trout, an opinion that is disputed (C. L. Hubbs, pers. comm.). The systematic status of this form awaits resolution through further studies.

Eagle Lake rainbow trout, *S. g. aquilarum*, is a brightly colored form adapted for living in the highly alkaline waters of Eagle Lake, Lassen County. They have been variously classified as a cutthroat trout subspecies (Snyder, 1933), as a rainbow trout subspecies, and as a hybrid between native cutthroat and introduced rainbow trouts (Hubbs and Miller, 1948). If they are in fact a native rainbow trout population they are a zoogeographic enigma, since all other fishes present in the lake are native to the Lahontan system from which rainbow trout are otherwise absent. The present-day form does seem to be like rainbow trout in most of its characteristics and, regardless of its origin, is uniquely suited for Eagle Lake.

Royal silver rainbow trout, *S. g. regalis*, supposedly native to Lake Tahoe and now extinct, presents a zoogeographic puzzle similar to that of Eagle Lake rainbow trout. However, there is little reason to doubt that J. O. Snyder's 1912 description of "*Salmo regalis*" was based on large-sized rainbow trout derived from fish introduced in the 1860s and 1870s. His royal silver rainbow trout differs little from rainbow trout of known origin that have grown to large sizes in other large lakes.

Identification. Rainbow trout are highly variable in color, body shape, and meristic characters. Nevertheless, they can usually be recognized as silvery trout with numerous black spots on the tail, adipose fin, dorsal fin, and back (best developed anteriorly) and an iridescent pink to red lateral band. The cheeks (opercula) are also pinkish, the back iridescent blue to nearly brown, the sides and belly silver, white, or yellowish. Resident stream forms are generally darker than lake or sea-run forms. The mouth is large, the maxillary usually extending behind the eye. The teeth are well developed on the upper and lower jaws, on the head and shaft of the vomer, on the palatines, and on the tongue. Basibranchial teeth are absent. The dorsal fin has 10 to 12 principal rays; the anal fin, 8 to 12 principal rays; the pelvic fins, 9 to 10 rays each; and the pectoral fins, 11 to 17 each. The tail is slightly forked. There are 16 to 22 gill rakers on each arch and 9 to 13 branchiostegal rays. The scales are small, with 110 to 160 pored scales along the lateral line, 18 to 35 scale rows above the lateral line, and 14 to 29 below it.

The coloration of the young is similar to that of the adults except that the young also have 8 to 13 widely spaced parr marks centered on the lateral line (the interspaces are wider than the parr marks), 5 to 10 dark marks on the back between the head and dorsal fin, white to orange tips on the dorsal and anal fins, and few or no black spots on the tail (McPhail and Lindsey, 1970). Adults from small streams may retain much of the color pattern of parr.

Names. Salmo is the ancient Latin name for the Atlantic salmon (*S. salar*) and is probably derived from the Latin verb meaning "to leap." *Gairdneri* is after Dr. Meredith Gairdner, a Hudson Bay Company naturalist who assisted Sir John Richardson in his collections of Columbia River fishes. The scientific name is frequently listed in the older literature as *Salmo irideus*, the name given to nonsteelhead by Gibbons in 1855. Synonymies of the scientific nomenclature can be found in La Rivers (1961) and Scott and Crossman (1973).

Distribution. Rainbow trout are native to Pacific coast streams from the Kuskokwim River in Alaska down to northwestern Mexico, plus a few interior basins. In California, they are native to coastal streams from the Los Angeles River system and the Ventura River north to the Klamath River. They are also native to most of the Sacramento-San Joaquin system. They have been introduced into most of the suitable waters to which they were not native over most of the world. They are now present in South America, Africa, India and southern Asia, Japan, Europe, New Zealand, Australia, Tasmania, and Hawaii, as well as in most suitable waters of North America (MacCrimmon, 1971).

*Life History**. The life-history patterns of rainbow trout range from the highly migratory, sea-going pattern of steelhead populations, to the pattern of many isolated populations in small streams, where an individual trout may complete its entire life cycle in a few hundred meters of stream. When in fresh water, most rainbow trout are found in cool, clear, fast-flowing permanent streams and rivers, where riffles tend to predominate over pools. In the Sacramento-San Joaquin system they also inhabit the Squawfish-sucker-hardhead Zone in the larger streams, even though temperatures may often approach the maximum they can withstand. Mountain lakes and the cold, deep waters of reservoirs also provide suitable habitat for rainbow trout, but such populations have to be artificially maintained if suitable spawning streams are lacking. Rainbow trout will survive temperatures of 0 to 28°C. They can withstand temperatures at the upper end of this range, however, only if they have been gradually acclimated to them and if the water is saturated with oxygen. Optimum temperatures for growth and for completion of most stages of their life history seem to be 13 to 21°C. At low temperatures, they can withstand oxygen concentrations as low as 1.5 to 2.0 ppm but normally concentrations close to saturation are required for growth. Their tolerance of the varying chemical conditions of water is also broad. They can live in water ranging in pH from 5.8 to 9.6. All other factors being equal, best growth seems to be achieved in slightly alkaline waters (pH of 7 to 8), although Eagle Lake trout have adapted to the highly alkaline waters of Eagle Lake (ph of 8.4 to 9.6).

While rainbow trout are the only fish species found in many California streams, more often than not they occur with other salmonids (especially brown trout and juvenile coho and chinook salmon), sculpins (*Cottus* spp.), speckled dace, suckers (*Catostomus* spp.), and Sacramento squawfish. It is unusual, however, to find more than three to four other species in abundance where rainbow trout are common. Rainbow trout are fairly flexible in their behavior and habitat requirements. They can interact successfully with other species of fish, avoiding as much as possible direct competition for food and space. In coastal streams, juvenile steelhead interact with juvenile coho and chinook salmon and, as a result, the species select different microhabitats (Hartman, 1965; Everest and Chapman, 1972). When brown trout and rainbow trout are found in the same stream, brown trout tend to select slow, deep pools with lots of cover, while rainbow trout select the faster water (Lewis, 1969). Rainbow trout also tend to feed more on drift organisms, while brown trout feed on the bottom. The interactions between rainbow trout and various nongame species are discussed in the ecology chapter of this book.

One of the main reasons rainbow trout are so successful at interacting with other fish species is that they are highly aggressive and defend feeding territories in streams. Other salmonids recognize the aggressive displays of rainbow trout (e.g., rigid swimming, flared operculae, nipping at the caudal peduncle of invading fish) and usually react either by fleeing or by challenging the trout with similar displays, perhaps driving it off its territory. The winners of such interspecific contests are determined by

*The literature on rainbow trout life history is so large, even just for California populations, that a literature review is far beyond the scope of this book. This summary is based largely on personal experience (e.g., Moyle and Nichols, 1973), the compilations of McAfee (1966), Carlander (1969), and Scott and Crossman (1973), the monograph of Shapovalov and Taft (1954), and the papers in Northcote (1969).

a number of factors, but relative size and habitat preferences play leading roles. Rainbow trout can generally drive nongame fishes such as suckers and squawfish, which do not respond to the displays themselves, from feeding territories by repeatedly rushing at the invaders and nipping at their sides and caudal peduncles (H. Li, pers. comm.).

Territorial displays are also extremely important in the intraspecific interactions of rainbow trout. In streams, rainbow trout set up feeding territories which they defend from each other. The number of territories depends on many factors, but probably the most important are size of the fish, speed of current, water temperature, and availability of cover. Superimposed on this territorial mosaic, however, is a dominance hierarchy in which larger fish are dominant over small fish and hold much larger territories. The smaller fish may actually hold small territories within the territory of the large fish. They interact with each other and a stable hierarchy develops to the point where they will actually help the dominant trout defend the entire territory against invading trout (Jenkins, 1969). These territorial interactions may be the most important factor limiting the number of trout in many streams, outweighing food availability.

The competitive interactions of rainbow trout with each other and with other fish species in lakes is less well understood than it is in streams. The trout tend to school and wander about within lakes, so aggressive behavior probably plays a minor role. The numerous observations of decrease in trout growth rates and population size following the introduction of another species (usually a cyprinid) into a pure trout lake, indicates, however, that direct competition for limited food resources takes place initially. Eventually, the trout and the new species will segregate by habitat and feeding strategies and the trout may subsist in part by preying on the other species. A classic, well-documented case of this sort is Paul Lake, British Columbia (Johannes and Larkin, 1961).

In the summer months, stream-dwelling rainbow trout feed mostly on drift organisms, but they will also take active bottom invertebrates. Thus, the stomachs from a sample of trout taken from one stream at the same time are likely to contain a hodgepodge of terrestrial insects, adult and emergent aquatic insects, aquatic insect larvae, amphipods, snails, and occasional small fish. Individual trout, however, tend to specialize in the type of organisms they feed on, even over a long period of time, and do not take the whole range of foods available (Bryan and Larkin, 1972). In the winter, feeding is considerably reduced over summer levels and the trout feed mostly on bottom-dwelling invertebrates. The most commonly taken bottom invertebrates at all seasons are either those that drift on a regular basis (e.g., baetid mayfly larvae, amphipods), those that are active bottom crawlers or live in exposed positions, or those that are large in size. The size of the organism taken tends to increase with the size of the feeding fish. Rainbow trout can feed at virtually any hour of the day or night but feeding activity is usually most intense around dusk.

In lakes, feeding varies with invertebrate availability. Although benthic invertebrates and zooplankton seem to be preferred, terrestrial insects will be taken in numbers when other foods are scarce. Rainbow trout in lakes also have a greater proclivity for feeding on fish than do stream-dwelling rainbows, although fish normally do not become an important item in the diet until the trout are 30 to 35 cm TL. Thus, large Eagle Lake trout subsist mostly on tui chubs, while trout in California reservoirs subsist on threadfin shad or delta smelt. Other fishes commonly eaten in California are sculpins and suckers. As in streams, feeding is most intense during the summer but can continue throughout the winter, at temperatures as low as 1°C (Elliott and Jenkins, 1972). Steelhead feed on estuarine invertebrates after they leave their home streams but fish gradually become more important in their diet as they increase in size. The large size and rapid growth achieved by steelhead, and to a lesser extent by lake-dwelling rainbow trout, can be attributed in a large part to their diet of fish.

Growth rates in rainbow trout are variable. In mountain lakes, they reach 11 to 17 cm TL in their first year, 14 to 21 cm TL in their second, and 20 to 23 cm TL in their third. In such lakes they seldom live longer than six years or grow over 40 cm TL. Growth rates are similar in small California streams. The most rapid growth in California is achieved in large lakes and reservoirs. In Eagle Lake, trout 20 to 23 cm TL are one year old, 43 to 46 cm TL are two years old, and 46 to 56 cm TL are three years old. Similar growth is achieved by fish planted as fingerlings in some reservoirs (e.g., Crowley Lake, Mono County) but generally it is somewhat slower, especially after the first year. Juvenile steelhead migrate out to sea at one to three years of age, at 13 to 25 cm TL. After one to two years at sea they return at 38 to 69 cm TL (1.4 to 5.4 kg). The largest known nonsteelhead rainbow trout, from Jewel Lake, British Columbia, weighed 23.9 kg (Hart, 1973), although the largest caught by angling (from Lake Pend Oreille, Idaho) weighed 16.8 kg. The largest such fish from California (Feather River) weighed 9.6 kg, while the largest California steelhead known (Smith River) weighed 9.7 kg (Anonymous, 1964). The largest steelhead on record, from Alaska, weighed 19.1 kg (Hart, 1973). The oldest rainbow trout known are those from Eagle Lake, at eleven years. Steelhead occasionally reach nine years old, but the maximum age for most nonsteelhead rainbow trout is seven years.

Most nonandromous rainbow trout mature in their second or third year, but the time of first maturity can vary from the first to the fifth year of life. Mature fish can be of any size from 13 cm on up. Most steelhead spawn for the first time after spending two to three years in fresh water and then one to two years in salt water. However, spawning fish, usually small males, that have spent only one year in each habitat do occur on a regular basis in some streams.

Most wild rainbow trout are spring spawners, from February to June, but low temperatures in high mountain areas may delay spawning until July or August. California steelhead trout also spawn in the spring, but they frequently migrate upstream in the fall several months before they actually spawn. In some north-coast streams, small numbers migrate upstream in the late spring, spend the summer in deep pools, and spawn in the spring of the following year. Steelhead and other rainbow trout have well-developed homing abilities, and usually spawn in the same stream and area in which they had lived as fry. This means that local races of trout tend to develop that are adapted to local conditions.

Successful reproduction of rainbow trout generally requires a gravel riffle, in which a redd can be dug by the female and the eggs successfully incubated. Spawning behavior is similar to that of brown trout. The number of eggs laid per female depends on the size and origin of the fish but ranges from 200 to 12,000 eggs. Rainbow trout under 30 cm TL typically contain less than 1,000 eggs, while steelhead contain about 2,000 eggs per kg of body weight. Both rainbow and steelhead usually spawn once a year, but it is not unusual for fish to skip a year between spawnings.

The eggs hatch in three to four weeks (at 10 to 15°C) and the fry emerge from the gravel two to three weeks later. The fry initially live in quiet waters close to shore and exhibit little aggressive behavior for several weeks.

Status. Rainbow trout are the most popular and widely distributed gamefish in California. The demand for them is far beyond the natural reproductive capacities of wild populations, so a considerable portion of the fishing-license revenues of the California Department of Fish and Game goes towards supporting hatcheries that rear domestic strains of rainbow trout for planting on a put-and-take basis. Most trout planted are 18 to 20 cm TL and are caught within two weeks of planting (Butler and Borgeson, 1965). This is fortunate because hatchery-raised fish are ill-adapted for surviving in streams and are likely to die of starvation or stress within a few weeks anyway. Mortality is highest when they are planted in relatively small numbers in a stream that also sustains a wild trout population, because the planted fish will be unable to break into the established dominance hierarchies of the wild trout. If large numbers are planted over a wild trout population, the effect of the sheer numbers is likely to disrupt the established hierarchies, making the wild fish more vulnerable to angling. Such streams generally have to be continually planted if any sort of trout fishery is to be sustained, since neither the wild nor domestic trout can maintain themselves very easily.

In lakes, the survival rates of planted fish are much higher than they are in streams because of the absence of dominance hierarchies in wild fish, the low expenditure of energy required to stay alive (and become adjusted to the environment) in the absence of current, and the lower vulnerability of the fish to angling. In lakes, it is often economical to plant fingerling trout in place of catchable size fish, which it seldom is in streams.

Despite the generally low survival rates of planted trout, especially in streams, a few often will survive and interbreed with wild trout. Thus, indiscriminate planting of rainbow trout has led to loss through hybridization of many distinctive local populations, not only of rainbow trout but of other closely related species such as golden trout, cutthroat trout, and redband trout. Only in recent years has the aesthetic value of distinctive local populations been recognized and efforts made to preserve the few that are still left.

Another problem of some concern to fisheries managers in California is the long-term decline of steelhead populations. The decline is largely attributable to degradation of the spawning streams through sloppy logging, dewatering, dam construction, and pollution. Hatchery production of young steelhead can compensate in part for the loss of naturally spawned fish but it cannot compensate for the loss of the streams.

References. Anonymous, 1965; Bryan and Larkin, 1972; Butler and Borgeson, 1965; Carlander, 1969; Elliott and Jenkins, 1972; Everest and Chapman, 1972; Fry, 1973; Hart, 1973; Hartman, 1965; Hubbs and Miller, 1948; Jenkins, 1969; Johannes and Larkin, 1961; La Rivers, 1962; Lewis, 1969; McAfee, 1966; MacCrimmon, 1971; Moyle and Nichols, 1973; Needham and Gard, 1959; Northcote, 1966; Schreck and Behnke, 1971; Scott and Crossman, 1973; Shapovalov and Taft, 1954; Snyder, 1933; Wales, 1939.