

UC Davis

San Francisco Estuary and Watershed Science

Title

Biology, History, Status and Conservation of Sacramento Perch, *Archoplites interruptus*

Permalink

<https://escholarship.org/uc/item/8st5q6df>

Journal

San Francisco Estuary and Watershed Science, 9(1)

Authors

Crain, Patrick K
Moyle, Peter B

Publication Date

2011

DOI

<https://doi.org/10.15447/sfews.2011v9iss1art5>

Copyright Information

Copyright 2011 by the author(s). This work is made available under the terms of a Creative Commons Attribution License, available at <https://creativecommons.org/licenses/by/4.0/>

Peer reviewed

Biology, History, Status, and Conservation of Sacramento Perch, *Archoplites interruptus*: A Review

Patrick K. Crain¹ and Peter B. Moyle

Center for Watershed Sciences and Department of Wildlife, Fish, and Conservation Biology
University of California, One Shields Avenue, Davis CA 95616 USA

ABSTRACT

This paper is a review of the biology of Sacramento perch (*Archoplites interruptus*) based mainly on recent studies of their distribution, ecology, physiology, and genetics. The Sacramento perch is the only member of the family Centrarchidae that is endemic to California. It is most closely related to the rock basses (*Ambloplites* spp.) and is thought to have split from its eastern cousins during the Middle Miocene Period (15.5 to 5.2 million years ago, MYA). Their native range includes the Central Valley, Pajaro and Salinas rivers, tributaries to the San Francisco Estuary (e.g., Alameda Creek), and Clear Lake (Lake County). Today, they are most likely extirpated from all of their native range. They are known to persist in 28 waters outside their native range: 17 in California, nine in Nevada, and one each in Utah and Colorado. Disappearance from their native range coincided with massive changes to aquatic habitats in the Central Valley and with the introduction of alien species, including other centrarchids. Unfortunately, many populations established outside their native range have also disappeared and are continuing to do so.

Sacramento perch bones are abundant in Native American middens, and Sacramento perch were com-

mon enough in the 19th century to be fished commercially in large numbers. By the late 1800s their decline was evident and by the early 1900s they were rare in fish surveys. Their historic habitats were apparently sloughs, slow-moving rivers, and large lakes, including floodplain lakes. Sacramento perch are adapted to withstand high alkalinities (10.6 to 11.0 pH), are eurythermal—with 16 to 23 °C being their optimal thermal range—and can persist within a wider salinity range (mean 24 to 28 parts per thousand, ppt) than other centrarchid species. Larval and juvenile oxygen consumption increases with age, size, and temperature, except at very low temperatures, where consumption is higher than in their optimal temperature range. In adult Sacramento perch muscle, oxygen consumption significantly increases with temperature. The diet of Sacramento perch varies with size of fish and availability of food by season, but they feed primarily on insect larvae when small, and on fish and macroinvertebrates when large. Growth rates differ in response to population density, diet, gender, water temperature, anthropogenic influences, and presence of alien species. They can grow up to 61 cm total length (TL) and 3.6 kg, with a maximum recorded age of 9 years. Females grow faster than males and have lower mortality rates after the first year of life. Sacramento perch breed for the first time during their second or third year of life. The number of gametes produced is similar to that of

¹ Corresponding author: pkcrain@ucdavis.edu

SAN FRANCISCO ESTUARY & WATERSHED SCIENCE

Lepomis and *Pomoxis* species (spp.) Spawning is initiated when water temperatures reach 18 to 28 °C from the end of March through as late as October. Males set up territories in littoral areas usually associated with aquatic vegetation, and guard them against other perch and potential egg predators. Courtship behaviors are similar to those of other centrarchid fishes. Sacramento perch eggs are deposited singly or in small clusters, are adhesive, and sink. Embryos hatch in approximately 27 to 72 hours after fertilization, and within 2 to 4 days the larvae are able to swim weakly. Larvae at swim-up are semi-pelagic or pelagic; small juvenile fish (15 - ≈50 mm) tend to shoal together in the littoral zone, moving into deeper water as they grow larger, with individuals becoming solitary or aggregating loosely together. We present two conceptual models of Sacramento perch life history: a reservoir-lake model, which fits their use of most present-day habitats, and a river model, representing their use of historic habitats.

Significant differences in genetic diversity were observed within and among eight Sacramento perch populations. The populations combined had fairly high diversity in genetic structure and were heterozygous for many alleles. However, only three of the eight populations were estimated to have effective population sizes greater than 50 and bottlenecks were detected in all but two of the eight populations. Differences among populations may have resulted from the size of founding populations and/or the genetic diversity of founding populations. Thus, a managed re-introduction strategy that favors genetic diversity should use individuals from all populations.

Our current knowledge of Sacramento perch biology indicates the following characteristics that are important for conservation:

1. They are adapted to using floodplains.
2. The mating behavior of males is divergent from that of their eastern counterparts.
3. Different life stages of Sacramento perch require different habitats.
4. They are presently limited in good part by interactions with alien centrarchid species.
5. Adults are limited by extreme water quality conditions, including high alkalinity.
6. Contaminants may have a major effect on reproduction, growth, and early life history.
7. Adults and juveniles are unable to maintain swimming velocities necessary to avoid being entrained in water diversions.
8. Introduced populations are limited by low genetic diversity.
9. Sacramento perch are exceptionally vulnerable to disease at warmer temperatures.
10. Most today live in artificial habitats, mainly reservoirs and ponds, which are not suitable for long-term survival.

Any strategy for re-establishing Sacramento perch must take multiple factors into account. We propose a conservation strategy that includes:

1. Ensure the future of all remaining populations by establishing backup populations from each source.
2. Establish a genetic management plan.
3. Establish a Sacramento perch experimental rearing facility.
4. Create a dispersed system of ponds for large-scale rearing and reintroduction into the wild.
5. Develop a strategy to build/use floodplain ponds for passive reintroduction.
6. Develop a source-sink reintroduction strategy by locating rearing ponds next to streams or sloughs.
7. Re-introduce fish into all habitats that seem to be suitable in their native range, including ponds and reservoirs.
8. Conduct a thorough search of Clear Lake to see if any Sacramento perch remain, so a special conservation effort for them can be established.
9. Develop and maintain an annual monitoring program for all known Sacramento perch populations.

10. Promote use of Sacramento perch in recreational fisheries.
11. Give Sacramento perch special status to emphasize the urgency of its recovery, beyond its present status as state Species of Special Concern.

KEY WORDS

Endemism, California, Centrarchidae, Sacramento perch, invasive species, Central Valley fish, fish conservation, fish translocation, fish life history

INTRODUCTION

The Sacramento perch (*Centrarchidae: Archoplites interruptus*) is endemic to the Sacramento-San Joaquin watershed, Pajaro and Salinas rivers, and Clear Lake (Lake County) of central California (Moyle 2002). It is listed as a Species of Special Concern by the California Department of Fish and Game (CDFG) and would probably be listed as a Threatened Species under both state and federal endangered species acts had it not been extensively translocated outside of its original range (Moyle 2002). The American Fisheries Society considers it to be a Threatened Species (Jelks and others 2008), whereas NatureServe lists them as Vulnerable (G3). It was included as a declining species in the Delta Native Fishes Recovery Plan (Moyle and others 1996). A priority of the CALFED Ecosystem Restoration Program (ERP) was to reintroduce the Sacramento perch back into its original range within the San Francisco Estuary. This interest resulted in a project that examined the basic biology of the perch, including its status, early life history, physiology, and the genetics of all extant populations (Crain and others 2007). Therefore, the purpose of this paper is to

1. Summarize what is known about the biology of Sacramento perch, including (a) history and taxonomy, (b) distribution and abundance, and (c) ecology and life history and (d) genetics.
2. Provide a conceptual model of Sacramento perch life history.
3. List gaps in our knowledge of Sacramento perch, expressed as a series of hypotheses.

4. Discuss restoration strategies and management, with a list of potential restoration sites.

This review synthesizes information from three major sources: (1) historic literature; (2) literature and personal communications from agency biologists from other states or areas that contain, or that previously contained, translocated populations; and (3) a recent University of California–Davis (UCD) study on their basic biology. Although our knowledge of Sacramento perch has increased greatly in the last few years, many unanswered questions remain as to why they have declined.

HISTORY, DESCRIPTION, AND TAXONOMY

History

The Sacramento perch is the only native member of the family Centrarchidae occurring west of the Rocky Mountains. Its isolation from other centrarchids dates back to the Middle Miocene period (15.5 to 5.2 MYA; Near and others 2005). Its fossil record is sparse, but it is one of the most numerous fish found in Native American middens in the Central Valley (Shultz and Simons 1973). The Sacramento perch was first discussed in Western culture in 1854 (Girard 1854). The following are important dates in the history of Sacramento perch and its habitats in relation to humans:

1852. Antoine Chabot begins hydraulic mining in California, which is the beginning of displacement of historic perch habitat within the Sacramento River and its tributaries (Holliday 1999).

1854. Charles F. Girard, a taxonomist at the Smithsonian Institution, describes the Sacramento perch as *Centrarchus interruptus* (Girard 1854).

1861. The California Legislature authorizes the Reclamation District Act, allowing drainage of Sacramento–San Joaquin–Delta lands and construction of sturdier levees, eliminating vast amounts of habitat previously occupied by perch (CDWR 1995).

1861. T. N. Gill (1861) assigns the Sacramento perch to its own genus, *Archoplites*.

SAN FRANCISCO ESTUARY & WATERSHED SCIENCE

1872. J. A. Poppe introduces common carp (*Cyprinus carpio*) from Germany into a pond in the Sonoma Valley; this species is found to prey on perch eggs and destroy spawning substrates (Dill and Cordone 1997).

1877. H. G. Parker translocates Sacramento perch from the Sacramento River to Washoe Lake, Nevada (Parker 1879).

1880. Further translocations are made within Nevada from Washoe Lake into Pyramid Lake and Walker Lake (Parker 1881).

1884. Fisheries for Sacramento perch are recorded in an early compilation by the United States Commission on Fish and Fisheries (Goode 1884): “It is abundant in the lower part of these [Sacramento and San Joaquin] rivers, large numbers being shipped to the markets in San Francisco. It is there bought and consumed mainly by the Chinese, who value it highly, paying more for it than for any other fish which they consume.” (p. 405)

1888–1899. Sacramento perch are noted as an important food fish in San Francisco fish markets with 40,000 to 432,000 pounds of fish harvested per year during this period (Skinner 1962). It is likely that these fish came from the lower Sacramento River and Sacramento–San Joaquin Delta.

1891. Largemouth bass are introduced into the Feather River and are the first non-native centrarchid to be spread throughout the state by anglers and biologists (Dill and Cordone 1997).

1895. Jordan and Gilbert (1895) find Sacramento perch in Clear Lake.

1896. Jordan and Evermann (1896) note that Sacramento perch are declining in abundance.

1908. C. Rutter (1908) finds Sacramento perch rare in surveys of Sacramento–San Joaquin Basin.

1908. Bluegill sunfish are introduced to California (Dill and Cordone 1997).

1913. J. O. Snyder (1913) finds Sacramento perch in the Pajaro River.

1930. Sacramento perch are described as abundant in Clear Lake (Coleman 1930).

1931. Neal (1931) notes that the perch are found “only in the few places where the non-native [fish] species are rare or absent.” (p.12)

1947. Clark Hubbs (1947) reports Sacramento perch from the Salinas River.

1950–1960s. Sacramento perch are found to be largely absent from the Delta in surveys by the California Department of Fish and Game (Turner 1966).

1960s. Sacramento perch are translocated to eight western states, with most originating from Nevada’s Pyramid Lake (McCarragher and Gregory 1970).

1960s. Sacramento perch are introduced into Crowley Lake (Mono County) (Fuller 2009).

1963. Sacramento perch are extirpated from Nevada’s Walker Lake, presumably in response to low water levels, which increased salinities to lethal limits (Cooper and Kock 1984).

1962. S. Mathews finishes his M.S. thesis on the age, growth, feeding, and reproductive habits of Sacramento perch (Mathews 1962), the first study on perch biology.

1965. Mathews (1965) describes reproductive behavior in Sacramento perch.

1966. A large survey of Clear Lake fishes turns up only nine Sacramento perch (Cook and others 1966).

1970. MaCarragher and Gregory (1970) find most introductions of perch into western states have not resulted in permanent populations, so continued stocking programs are needed to maintain the fisheries.

1973. Hopkirk (1973) finds no measurable differences among populations using meristics.

1974. Moyle and others (1974) describe the feeding habits of Sacramento perch.

1976. Sacramento perch are found occupying only a fraction of their original range in California, being limited to 14 small and disjunct bodies of water (Aceituno and Nicola 1976).

1976. *Inland Fishes of California* is published, which summarizes the published literature on Sacramento perch, citing 21 papers (Moyle 1976).

1979. UC Davis students find a remnant population still breeding in Clear Lake near Clear Lake State Park (Fong and Takagi 1979).

1979. Jack Johnson of Carson City, Nevada, catches a Sacramento perch for the California angling record in Crowley Lake, weighing 3 lbs., 10 oz. (CDFG 2008).

1980. Vanicek (1980) describes the decline of the Lake Greenhaven population and speculates that introduced centrarchid fishes (mainly bluegill) are the cause of decline.

1995. CDFG lists the Sacramento perch as a Species of Special Concern (Moyle and others 1995).

1999. Marchetti (1999) demonstrates that competition between bluegill and Sacramento perch can be a problem.

2002. *Inland Fishes of California*, revised and expanded, is published, and further summarizes published literature on Sacramento perch (31 papers cited, 10 published after 1976) (Moyle 2002).

2003. CALFED funds a study on basic biology at UC Davis.

Description and Taxonomy

Sacramento perch morphology is described in Moyle (2002).

Sacramento perch was originally believed to be an ancestral (“primitive”) form that split from eastern centrarchid species during the Middle Miocene period (15.5 to 5.2 MYA) (Near and others 2005). The first phylogenetic studies indicated that the Sacramento perch is most closely related to the flyer (*Centrarchus macropterus*) and crappies (*Pomoxis* spp.) (Maybee 1993). However, recent analysis using DNA sequences puts it as most closely related to rock basses (*Ambloplites* spp.) (Near and others 2004), which it resembles. Hopkirk (1973) found little meristic variation among populations of Sacramento perch. Nevertheless, the Clear Lake population was prob-

ably distinct because of its long isolation from other populations, a supposition supported by findings that other Clear Lake fishes are distinct (Hopkirk 1973; Aguilar and Jones 2009).

TRENDS IN DISTRIBUTION AND ABUNDANCE

Distribution

California

Sacramento perch are endemic to the Central Valley, the Pajaro and Salinas rivers, tributaries to the San Francisco Estuary (e.g., Alameda Creek), and Clear Lake generally at low elevations (<100 m) except for Clear Lake, which is at an elevation of 402 m. Today Sacramento perch are most likely extirpated from their native range. Moyle (2002) lists 28 localities in California, of which 11 are located in the Central Valley and one in Clear Lake (Table 1). The Central Valley localities consist of reservoirs and small lakes located outside their native valley-floor habitats, and so, presumably, all resulted from introductions. Recent surveys in Calaveras Reservoir (Santa Clara County) and Clear Lake were unsuccessful in finding any perch (P. Crain, UCD, unpublished data). Overall, Sacramento perch are known to still be present in five Central Valley waters, but all populations are small and unlikely to persist over the long term. They are already extirpated from four locations listed in Moyle (2002) and are possibly extirpated (though no recent surveys have been conducted) in two others.

Sixteen populations have been established in California outside their native range, although the status of four populations is unknown (Table 1). Sacramento perch exist in six California watersheds:

1. Clear Lake Reservoir in the upper Klamath basin, from which they have spread into the Lost River and then into the Klamath River from Link Dam down to Copco Reservoir.
2. The Cedar Creek watershed in the South Fork of the Pit River, including Moon and West Valley reservoirs down to the Pit 1 power station, although the only perch found outside the two reservoirs are juveniles representing larval escapes (Reid 2003).

SAN FRANCISCO ESTUARY & WATERSHED SCIENCE

Table 1 Major water bodies containing Sacramento perch in California in the 1990s, with a determination of status in 2008. Populations labeled unknown are most likely extirpated.^a

Location	County	Watershed (Sub-province)	Status in 2008
Clear Lake	Lake	Clear Lake	Unknown
Calaveras Reservoir	Alameda/Contra Costa	Central Valley	Extirpated
Alameda Creek gravel ponds	Alameda	Central Valley	Extirpated
Lake Anza	Contra Costa	Central Valley	Extirpated
Jewel Lake	Contra Costa	Central Valley	Present
Lagoon Valley Reservoir	Solano	Central Valley	Unknown
Hume Lake	Fresno	Central Valley	Present
Sequoia Lake	Fresno	Central Valley	Present
San Luis Reservoir	Merced	Central Valley	Present
Middle Lake	San Francisco	Central Valley	Extirpated
Almanor Reservoir	Plumas	Central Valley	Present
Butt Valley Reservoir	Plumas	Central Valley	Unknown
Abbotts Lagoon	Marin	North Coast	Present
Sonoma Reservoir	Sonoma	Russian River	Unknown
West Valley Reservoir ^b	Modoc	Pit River	Present
Moon Reservoir	Lassen	Pit River	Present
Honey Lake	Lassen	Lahontan	Unknown
Clear Lake Reservoir	Modoc	Upper Klamath R.	Present
Lost River and Tule Lake	Modoc	Upper Klamath R.	Present
Copco Reservoir	Siskiyou	Upper Klamath R.	Present
Sheepy and Indian Tom lakes	Siskiyou	Upper Klamath R.	Unknown
Bridgeport Reservoir	Mono	Lahontan	Present
East Walker River	Mono	Lahontan	Present
West Walker River	Mono	Lahontan	Unknown
Topaz Lake	Mono	Lahontan	Unknown
Gull, June, Silver, and Grant lakes	Mono	Mono Lake	Present
Crowley Reservoir	Mono	Owens River	Present
Lower Owens River, Pleasant Valley Reservoir	Mono	Owens River	Present

^a Source: Moyle (2002).

^b West Valley Reservoir and Moon (Tule) Reservoir are both in the Cedar Creek watershed, so are interconnected. The population was apparently extirpated in the 1980s when water levels were low and the reservoirs became ice-covered in winter. Sacramento perch were subsequently re-introduced (P. Chappell, CDFG, pers. comm.)

3. The Walker River watershed, including Bridgeport Reservoir and the Walker River below it (Moyle 2002).
4. The upper Owens River watershed including Crowley Reservoir, Pleasant Valley Reservoir and the Owens River (S. Parmenter, CDFG, pers. comm., 2005).
5. The Mono Lake watershed including June, Silver, Gull, and Grant lakes.
6. The Abbots Lagoon watershed including the upper, middle, and lower lagoons.

Sacramento perch apparently were once established in the Russian River, but were extirpated when the river's fishes were poisoned with rotenone by CDFG in the 1950s (Pintler and Johnson 1958). They may have been native to the Russian River, although early records are lacking. An attempt to re-establish them in the watershed was made in Sonoma Reservoir (Dry Creek drainage) when Sacramento perch were stocked from Abbots Lagoon (Point Reyes National Seashore, Marin County) and Clear Lake from 1985 to 1990 (Rick Macedo, CDFG, pers. comm. 2005). The status of this population is unknown, although anglers reported catching perch in the late 1990s (P. Crain, UCD, unpublished data).

Today, populations in just three California waters are considered to have long-term sustainability: Crowley Reservoir, Abbots Lagoon, and Clear Lake Reservoir. However, two of these populations exist in reservoirs, which are managed to provide water to public agencies so reservoir waters can be lowered to levels undesirable for perch. In addition, Crowley Reservoir is operated to generate power. Perch populations in Crowley today can be affected by the rapid lowering of water levels during the spawning cycle which leave nests stranded (Steve Parmenter, CDFG, pers. comm. 2005). This phenomenon also seems to be common in reservoirs managed for water storage. For example, lowering water levels in the spring in San Luis Reservoir (Merced County) apparently strands nests. Only when water levels remain high in the spring do good year classes of perch occur (Hess and others 1995).

Outside of California

Arizona. Arizona had only one introduction, made into a borrow pit near Buckeye (Maricopa County) in 1967 (McCarragher and Gregory 1970). It is reported to have spawned once but has not been reported since; it is presumed extirpated (Minckley 1973).

Colorado. Colorado's first Sacramento perch were released into Nee Grande Reservoir (Kiowa County) in 1964, with additional plants made into Newell Lake (Weld County) in 1965 and 1966 (McCarragher and Gregory 1970). Successive plants into small ponds and lakes in the same area (Banner 12 and 13, Lon Hagler Annex waterfowl pond) were made from Newell Lake (Imler and others 1975). Successive years of monitoring in Newell showed the establishment of a reproducing population by 1969 (McCarragher and Gregory 1970). One survey of Nee Grande Reservoir captured no perch and subsequently the lake dried up (McCarragher and Gregory 1970). Two Buttes Reservoir, stocked in the 1960s, has also dried up on several occasions since the introduction and subsequent sampling efforts show no Sacramento perch (Doug Krieger, Colorado Division of Wildlife [CDOW], pers. comm. 1998). Sacramento perch apparently exist in northeast Colorado, but its status is precarious. Fish were moved from the Lon Hagler Annex (Imler and others 1975) in an attempt to establish refuge populations. The first was in Abrams Lake, a privately owned, 50-acre lake near Berthoud. The second was in Gilberts Pond, a private pond south of Hygiene, adjacent to the Pella Crossing Open Space ponds owned by Boulder County. The third and final transplant was to a privately owned gravel pit pond near Fort Lupton. The success of the re-introduction into the first two ponds is unclear; transplanted fish were recaptured, but reproduction was not observed. The third transplant into the gravel pit produced multiple year classes with rapid growth in both juvenile and adult fish (Randy Vanburen, CDOW, pers. comm. 1998). Twelve Sacramento perch were moved from this pond into Milavec Reservoir to initiate a population there, but the status of this translocation is unknown (Harry Crockett, CDOW, pers. comm. 2005); perch are most likely not present.

Table 2 Status of translocated populations of Sacramento perch in Nevada in 2007

Location	County	Watershed (subprovince)	Status
Bassett Lake	White Pine	Steptoe Valley	Extirpated
Big Indian Lake	Churchill	Lahontan	Extirpated
Indian Lakes	Churchill	Lahontan	Rare
Harmon Reservoir	Churchill	East Walker	Rare
Lahontan Reservoir	Churchill/Lyon	Lahontan	Uncommon
Little Meadow Lake	White Pine	Spring Valley	Extirpated
Little Soda Lake	Churchill	Lahontan	Common
Little Washoe Lake	Washoe	Lahontan	Common
Pyramid Lake	Washoe	Truckee River	Uncommon
Rye Patch Reservoir	Pershing	Humboldt River	Uncommon
Sparks Marina	Washoe	Truckee River	Uncommon
Stillwater Marsh	Churchill	Lahontan	Common
Walker Lake	Mineral	Walker River	Extirpated
Washoe Lake	Washoe	Lahontan	Common ^a

^a Washoe Lake dries up periodically, but during wet years reconnects with Little Washoe Lake which doesn't dry up and restocks Washoe Lake with Sacramento Perch.

Nebraska. Introductions were made into Nebraska from reservoirs in eastern Nevada in 1961 (McCarragher and Gregory 1970). It was thought that Sacramento perch would be well adapted to the highly alkaline waters of the Sand Hills area, but populations had to be maintained by continual stocking. The combination of high alkalinity and temperature limited reproduction. The stocking program at Valentine Hatchery was suspended in 1962. In 1986, the USFWS at Valentine indicated that Sacramento perch no longer existed in local lakes, and that the species was on the verge of extirpation throughout the Sand Hills (Hrabik 1989). The Nebraska Game and Parks Commission (NGPC) regard Sacramento perch as extirpated from Nebraska (Dave Tunink, NGPC, pers. comm. 1998).

Nevada. Introductions were made into other states beginning in 1877 when perch were introduced from the Sacramento River into Washoe Lake, Nevada, then moved to Pyramid and Walker lakes in 1880. Sacramento perch were widely distributed in Washoe, Humboldt, Churchill, Lander, Eureka, and Elko counties (Parker 1881; Miller and Alcorn 1943). Of the

14 known introduction localities (Table 2), populations still persist in 10 of them. However, except for Pyramid and Little Washoe lakes, the long-term status of the populations is tenuous, given the state's emphasis on planting large predatory game fish, including striped bass, striped bass-white bass hybrids, and walleyes, in addition to the traditional warm water species such as centrarchid basses and sunfish (Sigler and Sigler 1987). Even Sacramento perch populations established in alkaline lakes that exclude most other fish species must be regarded as not secure, because if inflows are reduced and the water becomes too alkaline, perch will not reproduce (Woodley 2007).

New Mexico. Sacramento perch were stocked from unknown sources into Tres Lagunas or the Bottomless Lakes (Chaves County) which included Mirror Lake, Lea Lake, and Lazy Lagoon. Subsequent surveys failed to find any perch. They are considered extirpated from the state (Sublette and others 1990).

North Dakota. Introductions were made from Nebraska into North Dakota in 1963 into Round Lake (McHenry County) and Spiritwood Lake (Stutsman

County) (McCarragher and Gregory 1970). In 1964, Clear Lake and Lake Williams were stocked, presumably with fish from Nebraska. However, the transplants failed to establish populations and these lakes today are heavily stocked with other species (F. Ryckman, North Dakota Game and Fish Department [NDG&F], pers. comm. 1998).

Oregon. Sacramento perch were established in Oregon and the Klamath–Lost River System when CDFG introduced them into Clear Lake Reservoir (Modoc County, California) in 1966, using fish from the Central Valley Warm Water Fish Hatchery in Elk Grove (Moyle and others 1974). The perch spread down the Lost River into Tule Lake, and into the Klamath System from Link Dam (Lake Ewauna), downstream to Copco Reservoir in California. The perch are abundant in many areas where found (Roger Smith, Oregon Dept. of Fish and Wildlife [ODFW], pers. comm. 1998).

South Dakota. According to McCarragher and Gregory (1970) an introduction was made into White Lake (Marshall County) sometime in the early 1960s and 2 years of successful reproduction were recorded. However, no records of stocking Sacramento perch were found (records go back to 1941) for White Lake by the South Dakota Game Fish and Parks Department (SDGFP). A retired biologist admitted that wardens made many illegal introductions in that period, and that introductions could have been made by a federal agency with no state record (B. Hanteen SDGFP, retired, pers. comm. 2006). No Sacramento perch exist in South Dakota today (Brian Blackwell, SDGFP, pers. comm. 2006).

Texas. Sacramento perch were stocked in Hamlin Lake (Jones County) in 1966 from unknown sources (probably Nebraska). Fish surveys of the lake in 1969 turned up no perch and the lake was drained in 1971. Sacramento perch are considered extirpated from Texas (Ken Kurzawski, Texas Parks and Wildlife Department, pers. comm. 1998).

Utah. Sacramento perch were moved from one of the early Nevada populations to Utah into Pruess (Garrison) Reservoir (Millard County) and Cutler Reservoir (Box Elder and Cache counties) on the Bear River, although the exact timing is unknown

(La Rivers 1962). According to the Utah Division of Wildlife Resources (UDWR), the Garrison Reservoir population is still present, although in small numbers (Dale Hepworth, UDWR, pers. comm. 2006). Young-of-the-year perch were recently found in Minersville Reservoir—apparently the result of an illegal introduction—although the reservoir was largely drained in 2004 during an extended drought, so the perch are presumably extirpated.

Abundance

There are no historical records of Sacramento perch abundance, but the perch is one of the most common fish remains found in Native American middens in Central California (Shultz and Simmons 1973; Broughton 1994), in the Pajaro–Salinas Basin (Gobalet 1990, 1993), and near Clear Lake (Gobalet 1989). They were common enough to be recorded in commercial fish–catch records in San Francisco fish markets (Goode 1884; Skinner 1962). By the late 1800s, Jordan and Evermann (1896) noted that Sacramento perch were declining in abundance in the greater San Francisco Estuary. Rutter (1908) found them to be rare in his fish surveys of the Sacramento–San Joaquin Basin. Walford (1931) reported them as “not very abundant” (p 84). Curtis (1949) noted that the Sacramento perch had “declined greatly in numbers and, while it cannot be called rare, now plays a minor part in the sport fishery” (p. 265). During a year of intensive monthly sampling of the Sacramento–San Joaquin Delta, Turner (1966) reported catching nearly 12,000 centrarchids, of which just one was a Sacramento perch. Subsequent surveys of Delta fishes have produced only two Sacramento perch, one caught just above the junction of Little Potato Slough and the South Fork of the Mokelumne River in 1992 (I. Paulsen, CDFG, pers. comm. 1992) and one caught in Snodgrass Slough opposite the Delta Cross Channel in 2008 (C. Haagen, CDFG, pers. comm. 2008). The latter fish presumably originated from a transplantation experiment made in 2006. Recent surveys that failed to find perch include electrofishing surveys in 2008 aimed largely at centrarchids (L. Conrad, UCD, unpublished data). There is no systematic program of sampling for Sacramento perch in place today and estimates of

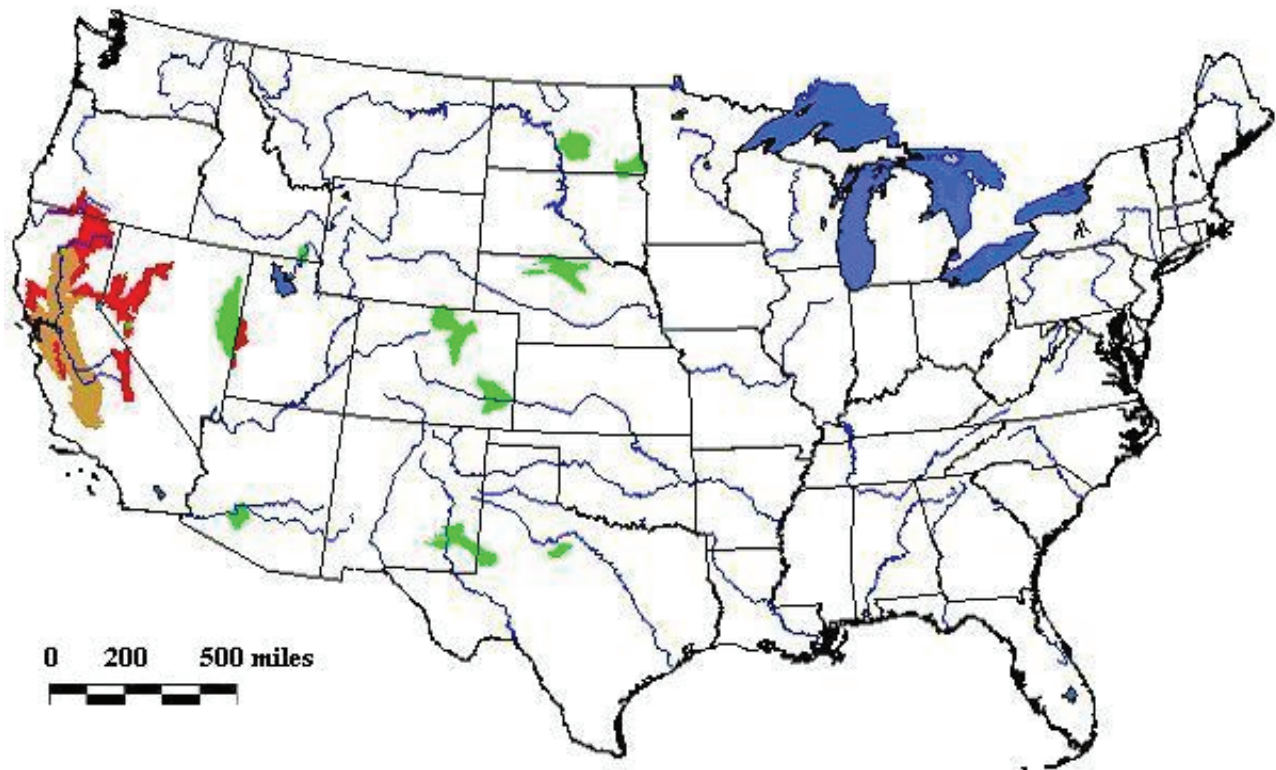


Figure 1 Watersheds into which Sacramento perch have been translocated. Red and green indicate translocations outside the original range (brown). Red translocations are still persisting and green translocations have been extirpated.

their abundance are mainly anecdotal. Crowley Lake has enough Sacramento perch to support an annual fishing derby, but no record exists on numbers of fish caught. Electrofishing surveys by CDFG in Lagoon Valley Reservoir put peak abundance at 1,500 per acre (CDFG 1996), but this reservoir has had no reproduction since 2002 (Wang and Reyes 2008). Recent surveys in Jewel Lake (1.1-ha reservoir) in the East Bay Regional Parks District (EBRPD) have estimated the population of Sacramento perch at 5,435 in 2004, 1,368 in 2005, but only 6 in 2006 (Pete Alexander, EBRPD, unpublished data).

Conclusions

Sacramento perch were once widely distributed and abundant in low elevation habitats in the Central Valley, the Pajaro–Salinas Basin, and in Clear Lake (Moyle 2002). Two populations (Clear Lake and Alameda Creek) that were previously thought to be

the only remnants of historic populations are now probably extirpated, although it is still possible a small population exists in Clear Lake. As of 2008, they were known to persist in 28 waters outside their native range: 17 in California, nine in Nevada, and one each in Utah and Colorado (Figure 1), although abundance estimates are lacking. None of the populations that exist in California just outside the peripheries of their native range are likely to persist indefinitely because they are in reservoirs or isolated ponds, subject to drying up, alteration, or introductions of non-native centrarchids. A similar situation exists for populations in other states. Only populations in the Owens River drainage, Walker River drainage, Pyramid Lake (Nevada), and the Klamath basin (Oregon and California), would seem to be large enough to have reasonable potential for persistence through the rest of this century, based on size and permanence of at least portions of the

waterways. However, the Pyramid Lake population is not entirely secure because water from the Truckee River is diverted and extirpation could occur (as it did in nearby Walker Lake) from increased alkalinities (Cooper and Koch 1984). Likewise, the other three populations exist in reservoir systems and could be threatened by altered water management practices or lowered water quality. The population in Abbotts Lagoon in Point Reyes National Seashore may also be able to persist, but the lagoon is small and isolated, and subject to large scale natural perturbation because it is located on the San Andreas Fault and connects to the Pacific Ocean.

In the past, it was assumed that Sacramento perch were not in danger of extinction because of translocated populations. However, its long term future is clearly not secure because: (1) it is extirpated from its native range; (2) all populations in California outside its native range are in highly altered or artificial water bodies; (3) all except 10 translocations in other states have failed, with only two populations not in danger of extinction in the near future (Pyramid Lake, Nevada and Lost River basin, Oregon). As in California, most extant populations occur in reservoirs and, thus, are subject to anthropogenic uses of water.

Overall, the Sacramento perch is gone from its native range, and its distribution and abundance outside its native range will continue to shrink as isolated populations become extirpated. Except for Nevada and Oregon, the websites of fisheries agencies in states other than California suggest little interest in Sacramento perch. This portends the continued loss of 'back up' populations and the loss of remaining genetic diversity.

ECOLOGY AND LIFE HISTORY

Habitat

The Sacramento perch was originally one of the dominant piscivorous fishes in the Sacramento-San Joaquin River system. The historic habitats of Sacramento perch were apparently sloughs, slow-moving rivers, and large lakes, including floodplain lakes (Moyle 2002). Many of these habitats became

very warm and alkaline during periods of drought (or even in late summer in normal years), which led to the early perception that Sacramento perch could adapt to withstand such conditions. In fact, Sacramento perch generally survive in adverse conditions, which include high alkalinity and salinity (McCarragher and Gregory 1970; Imler 1976; Moyle 2002; Woodley 2007) (Table 3), but this does not mean that these conditions are optimal. This perception, nevertheless, led to perch being translocated into highly alkaline (pH) waters throughout the west as game fish (McCarragher and Gregory 1970). Today, they are found primarily in reservoirs and ponds, and much of what we know about apparent habitat preferences comes from introduced populations in such artificial habitats. Here, we discuss what we can infer about their preferred natural habitats from observations of their basic ecology and physiology.

Structure. The deep body shape of Sacramento perch suggests they require structure for cover, including aquatic plants, downed trees, and submerged objects such as boulders, especially in shallow (<2 to 3 m) water. Presumably, this is both for protection from predators and for ambushing prey. For example, in Crowley Reservoir, they are most commonly found in shallow flat areas among beds of submerged aquatic vegetation as well as along steep slopes among large submerged boulders (P. Crain and Christa Woodley, UCD, unpublished observations). In Pyramid Lake, Sacramento perch are associated with rocky areas (i.e., tufa tufts, rocky ledges, and breakwaters), all in inshore areas (<23 m) (Galat and others 1981). In contrast, in highly turbid reservoirs (e.g., Moon, West Valley and Clear Lake reservoirs) there appears to be little association with structure.

Alkalinity. Because Sacramento perch evolved in the highly variable conditions found in the Central Valley, including severe droughts, they are adapted to withstand high alkalinities (pH) that are associated with low lake and river levels, as well as with estuaries. In experiments with juvenile and larval Sacramento perch, Woodley (2007) found that they can persist in highly alkaline conditions, where critical pH maximum level (where the fish loses equilibrium at 12, 18, 23, and 26 °C) can range from 10.5 to 11.0 pH. This is similar to other California native fish-

Table 3 Water quality (in parts per million) where Sacramento perch have failed to survive translocation for less than one year^a

Lake	pH	Carbonate	Bicarbonate	Total Alkalinity	Sulfate	Chloride	Calcium	Magnesium	Sodium	Potassium	Total Solids	Survival (Days)
Colorado												
Nee granda	8.4	8	182	190	8,800	600	644	775	1,600	—	13,825	—
Nebraska												
By-Way	9.3	716	1,505	2,221	20	178	52	8	870	500	3,800	60–80
Diamond	9.8	922	1,163	2,085	106	68	20	—	1,150	950	4,018	1.7–2.5
Goose	9.4	520	1,440	1,960	48	320	45	12	700	510	3,350	65–69
Little Alkali	9.8	987	1,951	2,938	101	155	16	140	728	775	3,450	20–26
McKeel Pond-2	9.2	610	1,470	2,080	40	140	59	1	1,100	1,200	4,300	70–82
Smithys	9.6	680	1,760	2,440	85	182	56	30	743	570	3,350	110–124
Smithys Pond-1	9.3	960	1,850	2,810	72	160	22	20	810	600	3,900	2.2
Smithys Pond-2	9.6	1,140	2,941	4,083	190	240	38	8	2,000	950	5,400	38
W. Long Pond-2	9.3	590	1,480	2,070	60	110	—	—	—	—	2,850	240
New Mexico												
Lazy Lagoon	8.3	0	84	84	5,200	11,200	1,300	792	—	—	25,200	0.5
Lea	8.2	0	120	120	2,200	3,400	960	180	1,500	—	8,300	4–5
Mirror	8.2	0	130	130	3,900	4,800	970	390	3,900	—	15,500	0.2–0.3
North Dakota												
Lake George	9.4	1,026	776	1,802	12,000	2,600	12	770	5,500	—	15,300	4–10
Texas												
Hamlin	8.1	0	40	510	1,400	1,400	1,600	1,000	610	14	3,800	Unknown

^a McCarraher and Gregory (1970).

es that can live in highly alkaline waters. Sacramento perch were successfully introduced into Clear Lake Reservoir (Klamath Basin) where Klamath Lake tui chub (*Siphatales bicolor*), Klamath largescale sucker (*Catostomus snyderi*), and Klamath shortnose sucker (*Chasmistes brevirostris*) have elevated pH resistance, similar to Sacramento perch (10.8 ± 0.5 , 10.7 ± 0.4 , and 9.6 ± 0.4 , respectively) (Falter and Cech 1991).

Despite their ability to survive high alkalinity, Sacramento perch were extirpated from Walker Lake, Nevada, when total alkalinity reached $2,500 \text{ mg L}^{-1}$ (Cooper 1978; Cooper and Koch 1984). McCarraher and Gregory (1970) found that natural reproduction ceased in hatchery ponds in Nebraska when total alkalinity reached $\geq 2,000 \text{ mg L}^{-1}$. This is supported by the observations of increased tumors, and hardened ovaries and kidneys as total alkalinity increased to $1,500 \text{ mg L}^{-1}$ in Pyramid Lake and other areas (Vigg 1978; Woodley 2007).

Water Temperature. Previous studies (Knight 1985) and recent experiments (Woodley 2007) indicate that Sacramento perch are eurythermal, with 16 to 23 °C being the optimal thermal range for growth, depending on age and condition. This temperature range is cooler than for other centrarchid species, but higher than for California native fish species (Woodley 2007). In general, the critical maximum temperatures for larval and juvenile Sacramento perch are similar to those of other centrarchid species, although their endurance range above a given acclimation temperature is higher (Woodley 2007). In tests of critical minimum (CT_{min}) and maximum (CT_{max}) temperature (temperatures at which the fish lose equilibrium), larval Sacramento perch had a CT_{min} of 8.5 ± 1.2 °C and CT_{max} of 36.1 ± 0.5 °C (Woodley 2007). For juveniles, the CT_{min} was 7.0 ± 0.8 °C and the CT_{max} was 36.6 ± 0.6 °C (Woodley 2007). Juveniles show

low energetic costs when inhabiting water in the 18 to 23 °C range, which allows them to take advantage of warm littoral areas for foraging (Woodley 2007). Woodley (2007) observed in both Crowley Lake and Abbotts Lagoon that juveniles were found in warmer, littoral areas, whereas adults remained in cooler waters, except when spawning. In the laboratory, adult Sacramento perch reached thermal minima at <10.0 °C and maxima at 29.5 ± 0.4 °C (Woodley 2007). The maximum is lower than that of other centrarchids, which have CT_{max} values of 33.9 to 34.8 °C (Woodley 2007). Adult Sacramento perch maximum thermal resistance is similar to that of other California native fishes, which range from 21 to 29 °C (Woodley 2007). The actual critical minima for adult Sacramento perch is probably lower than that measured in the laboratory because the experimental apparatus was constrained to go no lower than 10°C (Woodley 2007). An example of this is in Crowley Lake, where perch survive temperatures of 5 to 10 °C in late March through April (Jellison and others 2003).

Behaviorally, adult Sacramento perch prefer temperatures of 18.5 ± 3.1 °C (independent of their acclimation temperature), which is lower than other centrarchid species and similar to other California native species (Woodley 2007). In culture, adults experience increased disease frequency and higher mortality at elevated temperatures (Woodley 2007). In the wild, at elevated temperatures, they presumably have reduced avoidance responses to predators, reduced ability to forage, and reduced resistance to disease compared to other centrarchids living at the same temperatures. One reason for success of Sacramento perch in Abbotts Lagoon is presumably that temperatures hover around preferred values all year around: mean temperature averaged 14.9 to 15.7 °C over a 10-month study (Saiki and Martin 2001) and 14.6 to 15.7 °C over a one-year study (Bliesner 2005).

Salinity. Juvenile and adult Sacramento perch showed greater salinity endurance (mean 24 to 28 ppt in 12 to 16 hrs) than other centrarchid species (Woodley 2007). Salinity resistance of juveniles at 12, 18, 23, and 26 °C was 28 ± 1.1 , 27.6 ± 1.0 , 26.1 ± 1.5 , and 24.3 ± 1.2 ppt, respectively. Salinity resistance generally increased with decreasing temperature and at

12 °C juveniles had greater resistance than adults (26.3 ± 1.5 ppt) (Woodley 2007). Sacramento perch larvae have been raised successfully in waters up to 10 ppt salinity (C. Miller, Contra Costa Vector Control Authority [CCVCA], pers. comm., 2007). Unlike other fishes, the ability to withstand higher salinity does not increase with age in Sacramento perch. Sacramento perch are not an estuarine-dependent species, such as Sacramento splittail (*Pogonichthys macrolepidotus*) and Delta smelt (*Hypomesus transpacificus*), but juveniles can persist in high salinity waters, which could be advantageous for living on floodplains (shallow, littoral regions that might experience high evaporation) or in estuaries (Woodley 2007). In Colorado, Sacramento perch survived and reproduced in chloride-sulfate waters with salinities of 17 ppt and in sodium-potassium carbonate concentrations of over 0.8 ppt. (McCarragher and Gregory 1970). Sacramento perch likely can frequent brackish water habitats, although their ability to survive in elevated salinities may require high energetic costs, so they are not frequently found in such areas (Woodley 2007). For example, Saiki and Martin (2001) found that Sacramento perch in Abbotts Lagoon (with three basins) had access to a wide range of salinities, but were found mainly in freshwater sections.

Dissolved Oxygen. Larval Sacramento perch increase muscle oxygen consumption with age; at 2 hrs post-hatch, 1 day post-hatch (dph), 7 dph at 26 °C, their consumption is $0.26 \pm .08$, 0.30 ± 0.10 , and $0.38 \pm .08$ mg O₂ g⁻¹hr⁻¹, respectively (Woodley 2007). Juvenile muscle oxygen consumption increases with increasing temperature, except at 12 °C at which it is greater than at 18 °C and 23 °C but less than at 26 °C (12 °C, $0.15 \pm .03$, 18 °C, 0.08 ± 0.01 , 23 °C, 0.10 ± 0.01 , and 26 °C, 0.18 ± 0.03 mg O₂ g⁻¹hr⁻¹) (Woodley 2007). In adult Sacramento perch muscle, oxygen consumption significantly increases with temperature (12 °C, 0.04 ± 0.01 ; 18 °C, 0.07 ± 0.01 ; 26 °C, 0.13 ± 0.03 mg O₂ g⁻¹hr⁻¹) (Woodley 2007). Overall, oxygen consumption of all life history stages is lower at a given temperature than that of other centrarchid species except for largemouth bass (Woodley 2007). The low oxygen consumption rates are reflected in the ability of Sacramento perch to withstand relatively

low dissolved oxygen levels in the water, especially at cool temperatures. This ability is an advantage in escaping stressful high temperatures in littoral areas by moving into deeper, cooler water even if dissolved oxygen levels are low. Movements of this type were observed in Crowley Lake and Abbots Lagoon where adult Sacramento perch moved inshore to spawn, but then moved into deeper waters afterward (Woodley 2007).

Flow. Sacramento perch have been described as preferring slow, slough-like, or lentic waters (Moyle 2002). Sacramento perch juveniles have a U_{crit} (critical swimming velocity: the maximum velocity a fish can maintain for a specified amount of time) that overlaps with other centrarchid species, but the values are 43% to 58% higher than those of white crappie (*Pomoxis annularis*), a species with similar morphology and size (Woodley 2007). In general U_{crit} increases with fish size, but in Sacramento perch U_{crit} decreases with size (Woodley 2007). During all life stages (larval, juvenile, adult) Sacramento perch swimming performance is affected by temperature (Table 4). At 12 °C the U_{crit} of larval fish is significantly lower than at 23 °C and 18 °C, which is significantly lower than at 23 °C (Woodley 2007). In juvenile Sacramento perch, U_{crit} is significantly lower at 12 °C than at 18 °C and 26 °C (Woodley 2007). Adult Sacramento perch are similar to juveniles in that U_{crit} is significantly lower at 12 °C than at 18 °C and 26 °C (Woodley 2007). This indicates decreased swimming efficiency with elevated temperatures for both life stages and no clear optima as shown by the larvae. The critical swimming speeds for each life stage become thermally stressed when the temperature is above 23 °C (Woodley 2007). These critical swimming speeds are most similar to what a riverine fish might experience. Higher critical swimming speeds displayed by larvae and post-larvae seem to indicate that they could maintain position during high flow periods when some historical spawning probably occurred on floodplains (Woodley 2007).

Diet

The diet of Sacramento perch varies with fish size and availability of food by season (Table 5), although our understanding of their diet is potentially incom-

Table 4 Comparisons of Sacramento perch swimming performance, at different life stages, expressed as U_{crit} (\pm SD)^a

Life Stage	Water Temp (°C)	U_{crit} (cm s ⁻¹)	Body Lengths per sec ^b	Standard Length (cm)
Larvae	12	10.64 (2.10)	5.41 (0.78)	1.58 (0.20)
	18	12.11 (2.17)	7.05 (0.98)	1.52 (0.26)
	23	14.91 (3.22)	8.52 (1.93)	1.46 (0.13)
	26	13.69 (1.73)	7.50 (1.16)	1.49 (0.20)
Juvenile	12	23.67 (1.52)	3.28 (0.12)	7.21 (0.31)
	18	31.53 (2.42)	3.75 (0.19)	8.43 (0.76)
	23	35.43 (2.50)	3.34 (0.94)	10.63 (0.94)
	26	37.04 (4.55)	3.59 (0.34)	10.35 (1.15)
Adults	12	34.50 (4.61)	1.52 (0.30)	23.30 (1.78)
	18	40.28 (4.10)	1.85 (0.41)	21.72 (2.53)
	26	43.70 (6.73)	1.80 (0.31)	24.29 (1.33)

^a Woodley (2007).

^b Calculated as the fish's U_{crit} divided by the fish's body length.

plete because most of our diet data was collected from studies outside their native range (Moyle and others 1974; Imler and others 1975; Aceituno and Vanicek 1976; Bliesner 2005; Crain and others 2007). At the larval stage, Sacramento perch eat prey items corresponding to their gape. This can include rotifers, small zooplankton, and early instars of mosquitoes and midges. Miller (2004) found that Sacramento perch ate mosquito larvae at a higher rate than western mosquitofish (*Gambusia affinis*), which are commonly used in California to control mosquito populations (Linden and Cech 1990). Crain and others (2007) found that in a pond population, cladocerans were the dominant food followed by copepods in diets of ≥ 8 mm larval fish. In small juveniles, amphipods were the most important food followed by chironomid larvae. Fish < 40 mm in Clear Lake fed primarily on copepods; as the fish grew, cladocerans became more prevalent in their diets (Fong and Takagi 1979). As Sacramento perch grow larger, aquatic insect larvae and pupae become increasingly important in the diet, especially chironomids (Moyle and others 1974; Imler and others 1975; Aceituno and Vanicek 1976). In Pyramid and Walker lakes, Nevada, Sacramento perch feed almost entirely on fish by the

Table 5 Stomach contents of different age classes of Sacramento perch from five localities, expressed as percent of total volume (Woodward Pond, Willow Creek, and Curved Pond) or percent of total weight (Pyramid Lake and Kingfish Lake)^a

Location	Month	Age Class	Length (mm)	Number	Ostracoda	Copepoda	Cladocera	Amphipoda	Chironomidae	Ephemeroptera	Hemiptera	Fish	Gastropoda	Aquat. Larvae	Terr. Insects
Pyramid Lake	7	0	49–77	12	—	—	—	72	4	—	4	<1	—	20	—
Kingfish Lake	9,10	0	98–124	15	—	41	51	—	6	—	—	<1	—	<1	—
Woodward Pond	6	0	13–29	45	—	46	7	—	46	—	1	—	—	—	—
Willow Creek	7	0	50–62	16	—	<1	2	6	26	18	11	—	—	37	—
Curved Pond	4,	0	8–15	39	—	12	64	10	2	—	—	—	—	12	—
Curved Pond	5	0	8–13	24	5	20	70	5	—	—	—	—	—	—	—
Curved Pond	6	0	21–43	64	—	4	5	47	7	9	—	1	—	27	—
Curved Pond	7	0	36–66	18	—	—	1	16	43	40	—	—	—	—	—
Lake Greenhaven	3,4,5	0	50–100	9	tr	10	1	—	61	1	13	—	—	14	—
Lake Greenhaven	7,8,9	0	50–100	10	tr	25	tr	—	75	—	—	—	—	—	—
Lake Greenhaven	11,12,1	0	50–100	17	5	5	44	—	43	—	—	—	—	—	—
Lake Greenhaven	3,4,5	1,2,3,4,5,6	110–305	28	—	tr	tr	—	72	—	tr	5	—	10	—
Lake Greenhaven	7,8,9	1,2,3,4,5,6	110–305	44	tr	5	tr	—	79	—	1	10	—	5	—
Lake Greenhaven	11,12,1	1,2,3,4,5,6	110–305	42	tr	tr	22	tr	38	—	tr	38	—	tr	—
Pyramid Lake	7	1	92–145	13	—	—	—	1	—	—	—	91	—	8	—
Kingfish Lake	4	1	95–129	15	14	72	8	—	1	—	—	1	—	4	—
Woodward Pond	2,3	1	92–144	16	4	<1	5	—	90	<1	<1	—	—	—	—
Woodward Pond	4	1	81–117	35	2	5	5	—	76	—	5	—	—	7	—
Woodward Pond	5	1	91–106	10	—	3	3	—	83	—	6	—	<1	5	—
Woodward Pond	6	1	91–145	79	—	<1	—	—	72	—	19	<1	7	1	—
Clear Lake Res.	7	1	78–141	8	—	—	—	4	4	35	18	26	—	9	3
Pyramid Lake	7	2,3	150–286	20	—	—	—	<1	—	—	—	99	<1	—	—
Pyramid Lake	7	4,5	268–337	10	—	—	—	—	—	—	—	99	1	—	—

^a Moyle and others (1974); Crain and others (2007).

time they reach 90 mm TL. Their prey is mainly tui chubs (*Siphatales bicolor*) followed by Tahoe suckers (*Catostomus tahoensis*) and smaller Sacramento perch; this diet probably accounts for the large size of perch found in these large lakes (Vigg and Kucera 1981). In smaller lakes and ponds, their diet consists primarily aquatic insect larvae and pupae throughout life, with only occasional fish or crayfish being consumed, although young-of-year may be heavily preyed upon by adults (Moyle and others 1974; Imler and others 1975). The diets of juveniles and adults

vary widely by location and season, showing opportunistic feeding (Tables 6, 7, 8). In Lake Greenhaven, chironomid larvae and pupae made up three-fourths of their diet, with fish and copepods making up the rest (Acietuno and Vanicek 1976). Likewise, in Woodward Pond, the diet was mainly chironomids, followed by water boatmen and snails. In Clear Lake Reservoir, their diet consisted of mayflies, fish, and water boatmen (Moyle and others 1974).

Feeding takes place whenever the opportunity presents itself either day or night, although Sacramento

SAN FRANCISCO ESTUARY & WATERSHED SCIENCE

Table 6 Major prey of Sacramento perch in Abbots Lagoon, Point Reyes National Seashore. Prey items were collected in June and November of 2001, and in January, April, and June of 2002. Fish stomachs (n = 299) were examined that ranged in size from 68 mm to 323 mm.

Prey Item	Lower Lagoon Basin			Middle Lagoon Basin			Upper Lagoon Basin		
	% Occurrence	% Number	% Weight	% Occurrence	% Number	% Weight	% Occurrence	% Number	% Weight
<i>Hyallela azteca</i>	25.0	0.6	5.0	73.2	18.3	18.2	49.6	29.3	15.6
Chironomidae larvae	0.0	0.0	0.0	52.5	5.2	5.9	74.0	20.6	9.0
Chironomidae pupae	0.0	0.0	0.0	49.5	5.5	6.2	57.0	6.2	6.1
Mysidae	87.5	82.1	4.7	22.2	1.2	0.0	5.4	0.5	0.0
<i>Daphnia</i>	0.0	0.0	0.0	78.3	57.0	25.1	28.0	19.6	7.9
Coenagrionidae	0.0	0.0	0.0	66.3	1.5	25.0	25.8	1.4	17.5
Corophium	25.0	0.7	28.4	53.0	5.5	5.5	2.2	0.2	0.0
Copepoda	0.0	0.0	0.0	19.2	1.6	0.1	34.4	7.3	0.9
Erpobdellidae	0.0	0.0	0.0	8.6	1.5	2.9	37.6	8.8	16.3
Fish	37.5	—	31.3	1.0	—	0.5	1.1	—	0.0
Sphaeromatidae	12.5	12.5	24.8	10.6	0.2	0.2	1.1	0.0	0.0
Asellidae	0.0	0.0	0.0	1.5	0.0	0.1	19.4	3.7	2.4
Other	0.0	4.1	5.8	0.0	2.5	10.3	0.0	2.4	24.3

^a Bliesner (2004).

Table 7 Percentage by weight (g) of prey consumed by six age classes of Sacramento perch in Abbots Lagoon^a

Prey Item	Age					
	0+	1+	2+	3+	4+	5+
<i>Hyallela azteca</i>	27.6	18.8	23.9	19.1	16.9	6.5
Chironomidae larvae	18.9	9.6	5.1	3.2	4.4	11.1
Chironomidae pupae	13.6	11.8	4.3	1.2	7.9	7.0
<i>Daphnia</i>	15.4	6.3	21.8	27.8	24.9	29.4
Coenagrionidae	7.2	14.4	25.9	26.8	22.6	30.2
Corophium	0.0	6.1	4.8	5.4	0.0	3.6
Hirudinea	11.3	28.3	10.9	7.6	14.4	1.5
Other	6.0	4.7	3.3	8.9	8.9	10.7

^a Bliesner (2004).

Table 8 Comparisons of growth of Sacramento perch from different waters^a

Location	Mean Fork Length at Annulus (mm)								
	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8	Age 9
California									
Lake Greenhaven ^a	84	163	203	239	286	312			
Lake Almanor ^a	59	122	172	172	217	282			
Lake Anza ^b	86	120	131	138	147	154			
Kingfish Lake ^b	115								
Clear Lake ^c	85	171	196	220					
Colorado									
Newall Lake ^d	94	174	231						
Nebraska									
Big Alkali Lake ^d	85	184							
Clear Lake ^d	129	189	238	278	318	330			
Hudson Lake ^d	117	176	214	236	251				
North Twin Lake ^d	144	186	219	243					
Walgren Lake ^d	130	189	224	278					
Nevada									
Indian Lakes ^d	70	124	176	216	261	303			
Lahontan Reservoir ^d	67	122	166	211	253	286	318	335	355
Walker Lake ^e	102–127	140–190	190–241	229–299	279–318	305–356			
Pyramid Lake ^e	76–127	127–180	178–254	229–305	279–343	305–356	324–368	381–394	394–406
Pyramid Lake ^e	99	158	221	261	299	325	346	371	382
Pyramid Lake ^e	137–224	186–267	219–300	252–333	312–355				
Washoe Lake ^d	67	99	127	154	211	256	278	306	
North Dakota									
Round Lake ^d	79								
South Dakota									
White Lake ^d	70	114							

^a Acietuno and Vanicek (1976).^b Mathews (1962).^c Murphy (1948).^d McCarraher and Gregory (1970).^e Vigg and Kucera (1981).

perch are often most active at dusk and dawn (Moyle and others 1974; Moyle 2002). Sacramento perch exhibit the ability to switch between prey items, and are selective, based in part upon the energetic costs of capturing prey (Vinyard 1982). Their ability to switch prey items is similar to that of pumpkinseed sunfish, whereas the maximum speed and energy production they generate during prey capture are most similar to green sunfish (Webb 1975; Vinyard 1980, 1982). Sacramento perch are more capable than either pumpkinseed or bluegill at efficiently capturing small evasive prey such as copepods (Vinyard 1980, 1982).

Age and Growth

Growth rates of Sacramento perch are highly variable, depending on environmental conditions (Table 8). At the end of years 1, 2, 3, 4, 5, and 6 fish are typically 6 to 13 cm FL, 12 to 19 cm 17 to 25 cm, 20 to 28 cm, 21 to 32 cm, and 28 to 36 cm, respectively (Moyle 2002). The oldest fish known (9 years) were from Pyramid Lake, at 38 to 41 cm FL. The largest perch recorded is 61 cm TL (Jordan and Evermann 1896) and the heaviest fish on record was a 3.6 kg perch from Walker Lake, Nevada (La Rivers 1962). The California angling record, however, is a 1.64 kg fish, from Crowley Reservoir—although a fish measuring 43 cm TL (weighing 1.95 kg) holds the angling record for Utah, and a 43.2-cm (2.22-kg) fish holds the Nevada state record. Growth is more in weight than length, with fish from Abbotts Lagoon having a power regression formula as the best fit for this relationship (Bliesner 2005). The length–weight relationship for Sacramento perch from Abbotts Lagoon is $W = 0.00003L^{2.0}$ ($r^2 = 0.97$) (Bliesner 2005). This relationship is similar to growth curves for most fishes, where younger fish tend to have greater growth in length, but older adult fishes grow more in weight. This indicates greater investment in reproduction by adults, as opposed to somatic growth (Crain and Corcoran 2000). Females grow faster than males and suffer lower mortality rates after the first year of life, so fish older than 4 years tend to be females in all populations (Mathews 1962; Aceituno and Vanicek 1976; Vigg and Kucera 1981; Moyle 2002) (Figure 2). This is the opposite of other centrar-

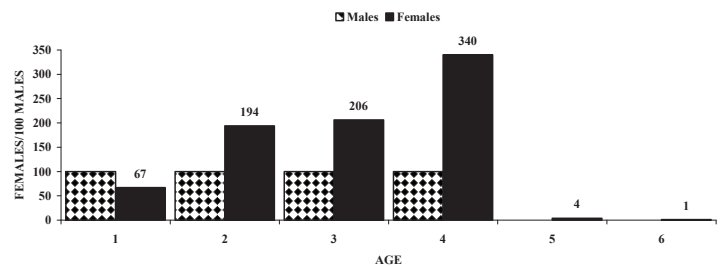


Figure 2 Number of females per 100 males in each age class of Sacramento perch from Pyramid Lake, Nevada. Source: Mathews (1962).

chids where largest fish are usually males, although small, short-lived males are present in many sunfish species as an alternative life history strategy (Moyle 2002). The increased proportion of females as perch age is presumably explained by the amount of energy expended by males in nest guarding, making them more susceptible to starvation and disease, as well as their increased vulnerability to predation at this time. In Crowley Reservoir, male perch were observed to become emaciated guarding their nests (Christa Woodley, UCD, unpublished observations).

Growth rates differ in response to population density, diet, gender, water temperature, anthropogenic influences, and introduced species. Sacramento perch populations that attain smaller sizes are generally found in small bodies of water in which temperatures exceed 20°C for extended periods of time (Woodley 2007). For example, the largest Sacramento perch in Curved Pond (0.4 ha) on the UC Davis campus was 187 mm FL and was age 4+ years. Pond temperatures averaged 22.6° from May to September (Crain and others 2007). Food for larger perch did not seem to be limiting; the pond also supports a large population of western mosquitofish, eaten by the perch, which peaks during the warmer months. In Lake Anza, perch growth slowed after the second year and six-year-old fish were only 150 mm FL, presumably because of the lack of forage fish for larger adults (Mathews 1962). Small fish size in Clear Lake where fish six to nine years old were 194 to 231 mm FL was attributed to competitive interactions with non-native fishes (Moyle 2002). In Lake Greenhaven, growth rates decreased following invasion of the lake by bluegill, which eventually resulted in the extirpation of the perch (Vanicek 1980).

Table 9 Estimates of fecundity of Sacramento perch females from Lake Anza and Pyramid Lake^a

Lake Anza, California				
Weight (gm)	Length (mm)	Age	Date (1961)	Number of Ova
37.5	120	II	June 21	9,860
42.7	136	IV	9	10,290
43.3	133	IV	9	9,750
48.5	141	III	May 16	8,820
48.7	140	IV	June 27	9,720
49.8	142	IV	1	8,370
51.0	138	III	21	10,530
51.7	140	III	9	10,270
52.9	132	III	1	13,970
54.2	144	III	May 25	11,000
56.4	144	IV	June 9	11,320
57.8	143	IV	21	16,220
58.0	152	IV	9	16,150
59.0	141	III	21	11,506
65.1	157	VI	21	14,100
71.5	153	III	May 16	11,155

Pyramid Lake, Nevada				
Weight (gm)	Length (mm)	Age	Date (1961)	Number of Ova
108	170	II	June 14	23,550
138	196	II	14	18,100
144	197	III	14	26,860
200	218	III	15	9,666
422	270	IV	15	54,460
425	254	III	15	79,630
435	273	IV	15	40,340
530	281	III	15	70,390
545	283	III	15	64,160
560	286	III	15	72,920
570	288	IV	15	93,090
635	300	IV	15	98,280
686	306	IV	15	94,220
705	312	V	15	90,800
810	331	V	15	124,720
850	337	V	15	121,570

^aMathews (1962).**Table 10** Temperature at which Sacramento perch first spawn in different states and localities

Location	Source	Period	Water Temp (°C)
California			
Clear Lake	Murphy 1948	Late May–June	17–28
Curved Pond	Crain and others 2007	Late March–June	18
Kingfish Lake	Mathews 1962	Early April	23
Lagoon Valley	Konyecsni 1962	Late March–mid April Mid May–late July	20–25
Lake Almanor	Aceituno 1976	Late May–early July	20
Lake Anza	Mathews 1962	Early May–mid July	20
Lake Greenhaven	Aceituno 1976	Late April–June	22
Shields Pond	Logan 1997	Late March–June	19
Colorado	Imler 1975	Mid June–August	22
Nebraska	McCarragher and Gregory 1970	June–October	25–28
Nevada			
Pyramid Lake	Vigg and Kucera 1981	June–August	20–24

Reproduction

Sacramento perch in general breed for the first time during their second or third year of life, although the smallest ripe fish found in Lake Greenhaven was a yearling female, 128 mm FL. The number of gametes produced is larger than in most centrarchid species, but similar to that of bluegill and crappie. The number of ova in sixteen females from Lake Anza (120 to 157 mm FL) ranged from 8,370 to 16,210 (mean 11,438); 16 females (196 to 337 mm FL) from Pyramid Lake contained 9,666 to 124,720 eggs (Mathews 1962) (Table 9). Spawning is initiated when water temperatures reach 18 to 28°C from the end of March through as late as October (Table 10). Males and females cultivated in captivity may spawn multiple times within the same season:

In one experiment, I had a pair [of Sacramento perch] spawn 18 times in a 148-day spawning trial (first spawn to last). Averaging 14,112 larvae per spawn for a female 158 mm SL, brood size ranged from 6,237 to 23,436. Another female, 162 mm SL, averaged 14,680 with a brood size ranging from 8,732 to 21,924 (seven spawns).

SAN FRANCISCO ESTUARY & WATERSHED SCIENCE

Another female, 168 mm SL, averaged 20,383 with a brood size 15,309 to 26,271 (six spawns). Temperature ranged from 23 to 29° C with most of the study running at the higher end 26 to 27 °C. The average interbrood interval was 9.6 days ranging from 5 days to 14 days between spawns. (C. Miller, CCVCA, pers. comm., 2010).

Whether or not this happens in the wild depends on several factors. Gonadal indices from Lagoon Valley Reservoir indicate a possible protracted spawning season beginning in late April through the first of August (Hallen, UCD, unpublished data). Older females seemingly spawn earlier in the season (Ridgway and others 1994), although spawning is early in most ponds and small bodies of water, probably a function of earlier warming (Crain and others 2007). When ready to spawn, males become darker than females, especially along the ventral surfaces and gill covers, which turn a purplish color, and distinct silvery spots show through the sides. Moreover, the males are darkest during the most intense periods of spawning (Mathews 1965). By comparison, females remain more uniformly silver. Before spawning, males congregate in shallow areas (15 to 60 cm deep) setting up territories (30 to 45 cm in diameter) before females arrive (Mathews 1962; Moyle 2002). In Crowley Lake males were seen to nest at depths of up to 300 cm (C. Woodley, UCD, unpublished data). These territories are usually associated with some type of aquatic vegetation such as pondweed; surfaces of rocks covered with algae, and submerged terrestrial vegetation (Crain and others 2007). In Clear Lake and Lake Greenhaven perch spawned on algae-covered riprap, but also over clay and mud substrates (Murphy 1948; Acietuno and Vanicek 1976). In Lake Anza and Kingfish Lake, perch spawned in depressions between submerged annual vegetation (grasses and forbs) (Mathews 1962). Sacramento perch seemingly prefer to spawn on or near vegetation, which could be an adaptation to spawning on floodplains.

However, perch are not confined to spawning on plants because they clean away debris and spawn in and around the edges of shallow depressions in a loose colonial fashion in Crowley Reservoir, similar to other centrarchid fishes (Christa Woodley, UCD, unpublished observations). In Kingfish Lake, a low-

density population of Sacramento perch spawned at evenly spaced intervals, with nests placed approximately every three meters apart (Mathews 1965). Murphy (1948) commented that in Clear Lake Sacramento perch remained in a shoal during spawning, and that 50 spawning fish were in a 1.2-x-3.7 m area; this would put nest densities at about one spawning pair per 0.2 m².

Once a territory (nest) has been set up, a male Sacramento perch guards his area against other male perch by chasing, nipping, and flaring opercular flaps (Mathews 1962; Moyle 2002). Other potential predators are also chased away from nesting areas; a bass placed in the nest was driven away repeatedly, although a hitch was ignored (Mathews 1962). When a salamander was placed in a nest the male perch was initially frightened off, but came back quickly and attempted to nudge the salamander from its nest. When the salamander was held in the nest, the perch attacked it, biting and striking its body, finally grabbing it by the leg and pulling it 30 to 40 cm from the nest (Mathews 1962). Males in territorial defense and courtship display often engage in a rapid burst of tail fanning starting with the head up, but ending with the head perpendicular to the bottom. They also engage in a yawning motion with their opercula as they patrol their nests, a characteristic centrarchid courtship display (Mathews 1962; Moyle 2002). Females also display the yawning behavior and become extremely active, contorting their bodies, rubbing against plants and other objects, and striking at other perch.

As a ripe female first approaches a male, she will be driven off by aggressive thrusts or a nip behind the gill flap. The female persists in her approach and can be attacked repeatedly for as much as an hour before the male accepts her as his mate (Mathews 1965). The pair then may spend approximately 30 minutes on the nest together before spawning occurs. During this time, the male frequently nips or nudges the female just in front of the vent, causing her to turn onto one side or the other. Male and female may nip at the bottom substrate and may pick up gravel or other benthic objects in their mouths, while undulating, contorting the body, gaping, and performing undirected biting (Mathews 1965). Descriptions of

spawning are somewhat different for wild fish and fish in aquaria (Mathews 1965). In the wild, both the male and female reclined to about a 45-degree angle, with their ventral surfaces close together and swim in a tight circle, facing in opposite directions; this was performed twice in 10 minutes and eggs were later found within the nest (Mathews 1965). In an aquarium, the female turned on her left side as she was nipped on the belly by the male. The female vibrated her body and fins several seconds before extruding eggs onto some plant roots; she was followed by the quivering male, which immediately turned on his side and fertilized the eggs. This happened four times in the space of 15 minutes, with the fish using both sides of their bodies. This behavior of male and female both turning on their sides is different from other centrarchid fishes where only females engage in this behavior (Mathews 1965). Males guard the nest for 2 to 4 days after spawning, allowing the eggs to hatch, but it is unlikely that all the larvae would be at swim-up stage when the nest is abandoned. This is in contrast to many other centrarchids where males guard postlarvae for a period of time even after they are able to swim (Winkleman 1996).

Early Life History

The eggs of Sacramento perch are spherical, with a mean diameter of 0.33 ± 0.04 mm reported in Leon and others 2008, although sizes of 0.85 mm, 0.9 to 1.1 and .8 to 1.0 mm have also been reported (Wang 1986; Wang and Reyes 2008; C. Miller, CCVCA, pers. comm., 2010). In other centrarchids, egg size varies by species, with rock bass having a mean egg size of 3.07 mm, pumpkin seed 1.50 mm, bluegill 1.47 mm, smallmouth bass 3.11 mm, largemouth bass 2.09 mm, and black crappie 1.27 mm (Cook and others 2006). The yolk is a yellowish to yellowish-white in color and is granular in texture (Wang 1986; Miller 2003). The oil globule is single and large, 0.11 mm in diameter in a 0.33-mm egg, 0.35 mm in a 0.85-mm egg and 0.3 to 0.4 mm in a 0.8- to 1.0-mm egg (Leon and others 2008; Wang and Reyes 2008; C. Miller, CCVCA, pers. comm., 2010). The chorion is transparent and elastic, with the perivitelline space being narrow in all stages (Wang and Reyes 2008). The fertilized eggs are deposited singly or in small clus-

ters and are adhesive to semi-adhesive (Wang 1986; Miller 2003), with the buoyancy being demersal or negative (Murpy 1948; Mathews 1962). Embryos hatch in approximately 19 to 36 hrs after fertilization, depending on temperature and within 5 days the larvae are able to swim weakly (Leon and others 2008). Newly hatched larvae are usually <4.0 mm TL (Wang 1986); 3.4 to 4.0 mm for specimens collected at Lagoon Valley Regional Park by Michael Dege with CDFG; 2.9 to 3.2 mm TL (Leon and others 2008); 2.5 to 3.2 mm TL from eggs obtained from Chris Miller, CCMVCD, and from the Tracy Fish Collection Facility Laboratory (Wang and Reyes 2008). Unlike other centrarchids, Sacramento perch larvae have a small filament that attaches the head of the larvae to the egg capsule, which can last 1 to 4 days. After the filament is absorbed, the larvae cling to the substrate for 2 to 4 days before swim-up (Miller 2004). The larval filament presumably allows larvae to remain attached to the substrate (e.g., submerged terrestrial vegetation) in flowing water (Figure 3).

Larvae at swim-up are semi-pelagic or pelagic; they may stay within inshore beds of aquatic vegetation or off-shore over beds of algae (C. Woodley, UCD,

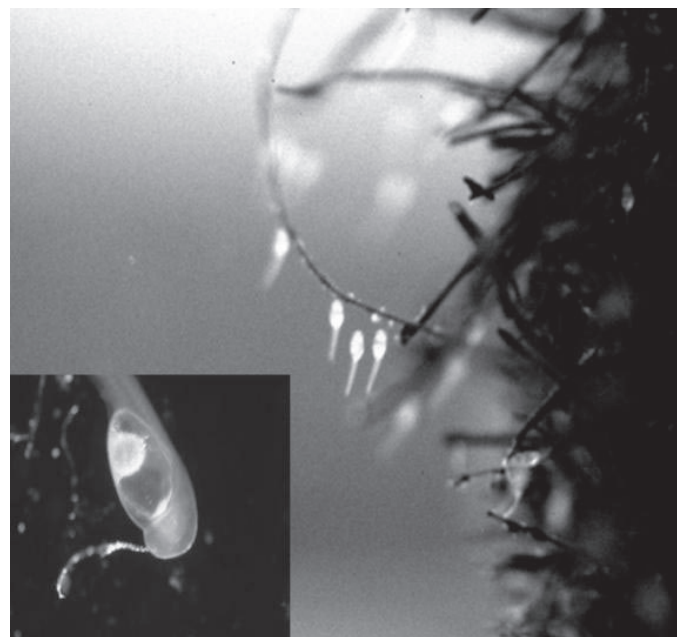


Figure 3 Sacramento perch larvae shown in close-up hanging by Spawntex® filament. Photo courtesy of Chris Miller, Contra Costa Vector Control Authority.

unpublished observations, 2006). Larvae can often be found in association with other fish larvae in macrophyte beds, including those of Sacramento blackfish, golden shiner, green sunfish, and largemouth bass (Matthews 1962; Wang 1986). Small juvenile fish (15 - ≈50 mm) tend to shoal together in the littoral zone, venturing into deeper water as they grow larger (Christa Woodley, UCD, unpublished observations). Eventually, shoaling behavior is replaced by individuals becoming solitary or aggregating loosely together, usually in association with some type of structure.

Causes of Decline

The disappearance of Sacramento perch from its native range coincided with massive changes to aquatic habitats in the Central Valley, combined with the introduction of a host of alien species, including other centrarchids. The mechanism of extirpation is presumably the result of interaction between changes to the environment and alien species. In addition, over-exploitation by 19th century fisheries and water-management practices may have contributed to its decline.

Habitat Change. Historically, Sacramento perch were abundant in major habitats of the Central Valley floor including large rivers, sloughs and floodplain lakes, terminal lakes, and the San Francisco Estuary. These habitats are among the most altered in California, having been drained, filled, rip-rapped, channelized, leveed, polluted, and generally made less suitable for native fishes. Sacramento perch were presumably hard hit by these changes because different life history stages require different but interconnected habitats. Thus the loss of appropriate shallow water habitat for juveniles, the reduction of cool, deep-water habitat for adults, and the loss of floodplain spawning areas helped to accelerate their decline. Some of the major habitats that have been lost include Lake Tulare in the San Joaquin Valley, which was drained for farming; the San Joaquin River, which was dewatered by diversions; and the Sacramento–San Joaquin Delta, which was converted from a vast floodplain-marsh to a complex of diked channels. Nevertheless, physiological studies (summarized in this paper) suggest that Sacramento perch can persist under extreme

environmental conditions that occur at least seasonally and our distributional studies indicate that they once lived in a wide variety of habitat conditions.

Alien Species. It is hard to evaluate the historic impacts of alien species on Sacramento perch populations because the perch were under pressure from hydraulic mining, habitat change, and fisheries when introductions were being made. However, even in the 19th century, the decline in Sacramento perch was attributed to alien fishes, especially carp and catfish, which were thought to prey on perch eggs (Jordan and Evermann 1896). This was the explanation usually given as perch continued to decline (Neale 1931; Curtis 1949). The general observation remains that when Sacramento perch are associated with alien fishes (especially centrarchids), their numbers decline, and, in most cases, extirpation occurs (Moyle 2002). For example, Sacramento perch were stocked into Sonoma Reservoir (Sonoma County) and were common in angler catches until bluegill and redear sunfish became abundant (P. Crain, UCD, unpublished observations).

There are a few exceptions to this rule, which is probably related to the kinds of alien fish present with the perch. Sacramento perch co-exist with largemouth bass in both Jewell Lake (EBPRD) and Abbotts Lagoon (Point Reyes National Seashore), in the absence of other sunfish and most other alien fishes. Sacramento perch thrive as an alien species themselves mainly in lakes and reservoirs that are too alkaline to support other centrarchids (see "Habitat," p. 11). But overall, the evidence indicates that Sacramento perch thrive in a diversity of habitats until alien fishes become abundant. The mechanisms responsible for this replacement are some combination of competition, predation, and disease.

Competition. In most places where they exist today, Sacramento perch feed largely on macroinvertebrates (Moyle 2002). Introduced sunfishes have similar diets and spatial needs during parallel life history stages. Marchetti (1999) found that in the presence of bluegill, Sacramento perch gain less weight and show reduced growth, when food is limited. Sacramento perch were found to be less aggressive than bluegill, although larger Sacramento perch were more

aggressive than smaller ones. Sacramento perch also shift their use of habitat in the presence of bluegill, tending to move out of deep cover (Marchetti 1999), which would make them more vulnerable to predation. Likewise, Bacon (1980) found that large Sacramento perch are less aggressive than small bluegill. These studies lend support to the hypothesis that aggressive dominance is the specific behavior that drives competition between Sacramento perch and bluegill. When relating the abundance of other centrarchid fishes to that of Sacramento perch, Vanicek (1980) found a significant negative correlation only with black crappie. The evidence overall indicates that where sunfish (*Lepomis* spp.) or crappie (*Pomoxis* spp.) are abundant, Sacramento perch do not persist.

Predation. Non-native predators can have devastating impacts on prey species that haven't co-evolved to resist their particular style of predation (Moyle and Light 1996). With the introduction of striped bass and largemouth bass into the San Francisco Estuary, a new source of predation was imposed upon juvenile and adult perch. However, it seems unlikely that these species preyed heavily on perch because of the abundance of so many other preferred soft-rayed prey species (minnows, shad, smelt). Murphy (1948) proposed egg predation by common carp and other species as a possible cause of perch decline. This hypothesis has still not been tested, and, in fact, carp and Sacramento perch rarely coexist. However, their incompatibility with bluegill (Moyle 2002) brings up the possibility that bluegill could prey on eggs and early life stages of Sacramento perch. Although male Sacramento perch guard their nests vigorously, they do so individually and would be no match for a school of bluegill intent on consuming eggs and fry (small juveniles). Carlander (1977) mentions that large male bluegill can prey on their own eggs and spawn early in the season, thus effectively eliminating early spawns. Bluegill also inhabit shallow beds of aquatic vegetation, which post-hatching Sacramento perch use as cover (Wang 1986); this suggests that bluegill predation on post-larvae and fry could be significant, especially if the bluegill are abundant and their own energetic demands are high (e.g. preparing for spawning). Even if bluegill and other sunfish do not prey directly on Sacramento

perch young, they could be a proximate cause of perch decline by driving the young from cover, making them more vulnerable to piscivores. This would not happen to adult Sacramento perch, which spend most of their time offshore in deeper water than bluegill.

Disease. Disease, although not documented within wild populations of perch, has been observed as a major problem when wild fish are brought in for experiments and hatchery production (C. Woodley, UCD, and K. Bliesner, Hayward State University [HSU], unpublished observations). Temperature and stress seem to play key roles in the contraction of disease, to which Sacramento perch may be highly susceptible, especially diseases brought in with introduced fishes. For instance, when adult Sacramento perch were acclimated to temperatures of 23°C and above, they continually contracted herpes-like viruses and were prone to outbreaks of common parasites such as ich (*Ichthyophthirius multifiliis*) (C. Woodley, UCD, pers. comm., 2007). When perch were acclimated back to lower temperatures (15 to 20 °C) and given antibiotics, the outbreaks subsided and eventually stopped; as soon as acclimation temperatures were raised again, the infections reoccurred. Common temperature for ich outbreaks were 15 to 25 °C, indicating that Sacramento perch had immune response difficulties at the elevated temperatures. Temperature-related disease responses may also play a major role in the survival of newly hatched perch. When hatched at 25°C, fry had a 10% survival rate as compared to 80% at 18 °C (C. Miller, CCVCA, and C. Woodley, UCD, unpublished data.).

Fisheries. Heavy fishing pressure was exerted on Sacramento perch in the middle to late 1800s. Sacramento perch were common in commercial catches, being surpassed only by salmon, white sturgeon and American shad in total catch (Skinner 1962). Heavy fishing pressure coupled with anthropogenic changes in landscape culminated in Sacramento perch being uncommon by the turn of the 19th century (Jordan and Evermann 1896). The only fishery today is a limited sport fishery, which the CDFG does not monitor. At present (2009), there is no limit on take of Sacramento perch in California waters, and there is at least one large fishery within

the state, in Crowley Reservoir. Each year thousands of Sacramento perch are taken during a “perch derby” in August. The reason given for the unlimited fishery in Crowley Reservoir is that Sacramento perch are not native to the area and therefore should not receive special protection (S. Parmenter, CDFG, pers. comm., 2007), although the same argument could be made for rainbow trout, the main focus of the fishery. The majority of the fishery occurs while perch are spawning, which generally runs from the end of May through early August. The impact of the fishery could be considerable if large females are removed regularly from the breeding population, thereby lowering egg production and year class recruitment.

Water Management Practices. Clearly reservoirs can support Sacramento perch, but most do not because of the combination of alien species and reservoir operation. Sacramento perch spawn in shallow water (usually 0.6-m to 3.0-m deep), so if water is drawn down during the spawning period, nests are likely to be stranded. This is why in abundant water years, large year classes of Sacramento perch occasionally develop in reservoirs that normally do not show good recruitment. An example of this phenomenon occurred in San Luis Reservoir in 1995; during a very wet spring, young-of-year perch were very abundant in the Portuguese Arm of the reservoir. This high abundance presumably happened because the reservoir stayed at its maximum capacity for much of the spring, thus allowing adult Sacramento perch access to shallow flats not normally available for spawning (Hess 1995). In most water supply reservoirs, water levels fall extremely fast, stranding nests and the embryos and larvae within them. In addition, rapid reservoir fluctuation eliminates beds of aquatic vegetation needed as cover by perch fry.

LIFE HISTORY MODELS

Here we present two alternative conceptual life history models of Sacramento perch life history, based on existing data and new knowledge gained from recent studies as summarized in this paper. The two models are a reservoir–lake model, representing most present-day habitats and a river model, representing presumed major habitats prior to disruption of

Central Valley rivers and their floodplains in the 19th century.

Reservoir–Lake Model

The success of Sacramento perch populations in reservoirs and lakes depends on minimizing their mortality as a result of predation by native and alien species (e.g., from lack of adequate cover), fluctuating water levels, variable food supply (especially insect larvae), poor water quality (especially temperature), and adverse behavioral interactions with alien centrarchids, at all stages of their life cycle. The life cycle is closely tied to their movement from deeper water into the littoral zone for spawning when temperatures reach approximately 16 to 28°C and daylight hours are approximately equal to nighttime hours. For this movement to work, the offshore areas must provide adequate food resources, protection from predators, and provide high water quality, including cool thermal refuges. The inshore areas must be deep and stable enough to allow for spawning and incubation of embryos, while also providing sufficient food and cover to protect larvae and small juveniles. Adults become mature at two years and live up to nine years, spawning annually. Both fecundity and growth rates are affected by the availability of appropriate prey (fish and macroinvertebrates), and so vary from region to region.

In spring (March through May), males move into the shallows ahead of females to establish territories that they guard vigorously against other males and intruders. They defend either prepared nests or patches of aquatic vegetation. Spawning may be repeated several times during the spawning season, which lasts for several weeks. The fertilized eggs are adhesive and stick to the substrate either singly or in small clusters. Flooded terrestrial vegetation or fairly open beds of aquatic macrophytes are preferred as spawning substrate, but other substrates used include, algae, algae-covered rocks, gravel, and mud. Embryos hatch in approximately 2 days and larvae remain attached to the chorion with a filament for another 4 to 5 days until swim-up occurs. At swim-up the larvae become nektonic and are found, often with other native larval fish, in vegetation or offshore in

association with submerged cover. The larval stage lasts approximately 2 weeks at which time the larvae settle to the bottom, shoaling together as fry in the shallows, usually near some type of cover. Juveniles shoal for approximately 2 months then become more solitary, moving out of the littoral zone into deeper water, where they rear until maturity.

River Model

Much like the reservoir-lake model, the river model depends on the same variables for successful year classes to develop, only with river flows setting water levels. The life cycle of Sacramento perch in rivers was presumably once closely tied to adult movement from the main channels and deep sloughs into shallow floodplains for spawning, when temperatures reach approximately 16 to 28°C and daylight hours are approximately equal to night-time hours. To be effective, river and slough habitat must provide adequate food resources, protection from predators, and high water quality, including cool thermal refuges. Males first move into sloughs adjacent to floodplains, most likely earlier than females, and then set up territories as floods offer the opportunity, similar to splittail (*Pogonichthys macrolepidotus*) (Moyle and others 2004). Spawning occurs on submerged terrestrial vegetation with embryos adhering to the substrate. The chorionic filament allows larvae to remain attached to the substrate in flowing water while yolk absorption is still taking place. At swim-up, the larvae are swept off the floodplain and into river channels or sloughs. After several days, the larvae settle into backwater or edge areas, where they shoal as fry. Alternatively, like splittail, the larvae remain in dense beds of flooded vegetation and leave the floodplain as fry, as flood water recedes. The fry seek out shallow areas that are warmer than the main river, which have beds of aquatic vegetation for cover. Taking advantage of abundant zooplankton and macroinvertebrates, they grow rapidly. As juveniles approach adulthood, they become more solitary and move to deep cool water in pools, oxbow lakes, and sloughs. Rivers and sloughs, with their complex habitats, including numerous fallen trees, historically provided abundant prey (macroinvertebrates, small fish),

protection from predators, and good water quality. Floodplains in most years had adequate water levels to allow spawning, incubation of embryos, sufficient food resources, and protection for larvae and small juveniles. However, it is likely that little such habitat was available in dry years, forcing fish to either forgo spawning or to spawn in marginal habitats to maintain minimal populations (as happens in splittail, Moyle and others 2004).

GENETICS

Understanding the genetics of Sacramento perch as a species requires understanding the genetics of isolated populations that resulted from a small number of introductions from limited sources. Schwartz and May (2008) collected genetic samples from eight populations from both California and Nevada and then analyzed genetic variation among populations. Twenty-three polymorphic microsatellite DNA loci were used for the study, based on their ability to be amplified reliably (Schwartz and May 2004). These loci were used to examine genetic variation and effective population size, to evaluate whether bottlenecks occurred during the movement of perch to other areas, and to measure the distinctness of alleles within populations.

Significant differences were observed by Schwartz and May (2008) in genetic diversity within and among populations. The eight populations together had fairly high diversity in genetic structure, being heterozygous for many alleles. Differences among populations may have resulted from the size of founding populations, the original genetic diversity of founding populations, or the number of founding individuals that contributed to the current population (Schwartz and May 2008). Only three of the eight populations—Abbotts Lagoon, Clear Lake Reservoir, and Pyramid Lake—were estimated to have effective population sizes larger than 50 individuals, the minimum recommended to prevent inbreeding depression (Schwartz and May 2008). Not surprisingly, genetic bottlenecks were detected in all but two populations: Abbotts Lagoon and Clear Lake Reservoir. This also suggests that most populations became established from a relatively small number of individuals.

SAN FRANCISCO ESTUARY & WATERSHED SCIENCE

Overall, populations of Sacramento perch collectively show a surprising amount of genetic diversity, indicating multiple introductions from different sources. Abbotts Lagoon and Clear Lake Reservoir populations had the highest genetic diversity and showed the least evidence of inbreeding (i.e., had the largest effective population sizes). Both also showed evidence of having had different origins (i.e., had more unique alleles than other populations). However, these two populations do not contain the entire genetic diversity of the species. Although a population from tiny Jewel Lake in Alameda County had a low overall genetic diversity, it was genetically the most distinctive of the populations.

HYPOTHESES: WHAT WE NEED TO KNOW ABOUT SACRAMENTO PERCH

Although many questions about the biology of Sacramento perch have been at least partially answered by recent studies, as summarized above, many questions remain to be answered, especially for effective conservation. This section lists a series of hypotheses (questions) under the following categories to show where information is needed to improve management strategies for Sacramento perch: floodplain use, reproductive behavior, life history strategies, effects of alien species, effects of water quality, genetics, and other potentially limiting factors.

Floodplain Use

Hypothesis 1: Adult Sacramento perch are adapted for using floodplains. There is some evidence that Sacramento perch once used floodplains for spawning, as our life history model indicates. It may be coincidence, but sharp declines in Sacramento perch populations occurred as most of California's floodplains became disconnected from their rivers.

Hypothesis 2: Juvenile Sacramento perch grow faster on floodplains than in adjacent sloughs and rivers. Floodplains provide optimal conditions for lower trophic-level production, where large amounts of decomposing vegetation coupled with warm water produce algae, bacteria, and ciliates. These, in turn, are food for rotifers, cladocerans, copepods, and

mosquito larvae, which can be fed upon by larval and juvenile fishes (Grosholz and Gallo 2006). Rapid growth on Central Valley floodplains has been demonstrated for Chinook salmon (Sommer and others 2001; Jeffres and others 2008) and other native fishes (Ribeiro and others 2005).

Hypothesis 3: Sacramento perch are preferential floodplain spawners. Without access to available floodplain habitat, they will spawn in other areas (lakes, reservoirs, ponds, rivers). However, it is possible that their greatest spawning success occurred when there were large expanses of floodplain available to them which not only provided space for spawning but food and cover for young. Species that show a similar pattern are Sacramento splittail and common carp.

Hypothesis 4: Sacramento perch have physiological, behavioral, and morphological adaptations to floodplains. The adhesive nature of their eggs, the filament that holds the larvae to the chorion, their preference for spawning in very shallow water, their ability to spawn on flooded annual vegetation, and the timing of their spawning in late March, when floodplains were historically available, all describe a fish adapted for floodplain spawning. In addition, adult perch can use their pectoral fins to maintain position in flow, and seem to respond to flow as a reproductive stimulus (C. Woodley, UCD, unpublished observations). Larvae and juveniles can survive in high salinity, high pH, and low dissolved oxygen—useful early life history strategies—if stranded in shallow floodplain lakes and ponds.

Reproductive Behavior

Hypothesis 5: Sacramento perch reproductive behavior diverges from that of other centrarchids. Sacramento perch males appear not to be as aggressive as their eastern counterparts in protecting their nests. Sacramento perch males do not create depressions for nests, but do clean an area. However, we are not certain if eggs are deposited into the swept area or on debris surrounding the swept area. Thus, the reproductive behavior of Sacramento perch seemingly diverges from that of other centrarchids, but many aspects of the behavior remain poorly documented.

Hypothesis 6: Sacramento perch males display alternative mating strategies. In addition to spawning by large dominant males, bluegill and other colonial nesting sunfishes exhibit alternative male strategies, such as sneaker and stalker males. This type of behavior may be present among loosely colonial nesting Sacramento perch (C. Woodley, UCD, unpublished observations) but needs to be confirmed.

Hypothesis 7: Sacramento perch give less parental care than other centrarchids. The level of parental care invested by Sacramento perch is poorly understood. Males guard the nests against predators and competitors, but seemingly with less vigor than other centrarchids and for shorter periods.

Life History Strategies

Hypothesis 8: Different life stages of Sacramento perch require different habitats. Ontogenetic shifts in perch habitat have been observed but poorly documented. Littoral habitats appear to be used by early life history stages. As they grow, perch seem to move into deeper waters, returning inshore only for reproduction. The reasons for these shifts and their relationships to perch decline are not understood.

Effects of Alien Species

Hypothesis 9: Sacramento perch are limited by interactions with alien (non-native) centrarchids. The gradual disappearance of Sacramento perch populations when forced to co-exist with bluegill, crappie, and other sunfishes indicates that interactions are a major cause of decline. Because adults and large juveniles of these species seem to co-exist, most interaction is likely to occur during early life history stages.

Hypothesis 10: Predation on embryos and juveniles by non-native centrarchids is a major source of mortality. Predation on embryos especially by adult bluegill males has been linked to lack of early recruitment. Sacramento perch, like many other California native fishes spawn early in the year (middle to late spring), so opportunistic predation on embryos and larvae by bluegill, common carp, and other alien fishes may be a major source of mortality.

Hypothesis 11: Juvenile perch are displaced from rearing habitat by adult sunfishes. Juvenile Sacramento perch may be dislodged from littoral habitat by larger adult centrarchid fishes, thus forcing them to use deeper and more open areas, leaving them more vulnerable to predation.

Hypothesis 12: Sacramento perch experience higher stress, slower growth, and lower rates of gonadal development in the presence of alien fishes, especially centrarchids. Sacramento perch may experience high levels of stress when trying to deal with unfamiliar alien fishes, especially large, aggressive species. In particular, competition between Sacramento perch and non-native centrarchids may be a major factor that limits Sacramento perch growth and reproduction. To manage for viable perch populations sources of stress need to be documented.

Effects of Water Quality

Hypothesis 13: Adult Sacramento perch are limited by extreme water quality conditions. Sacramento perch were apparently extirpated by lack of reproduction in Nebraska, New Mexico, and Nevada when alkalinities were at extreme levels. Yet the ability to survive under extreme conditions is the reason Sacramento perch was widely planted. This apparent contradiction needs to be better understood.

Hypothesis 14: Summer temperatures in most present-day Central Valley waters are sub-optimal for Sacramento perch. Adult Sacramento perch prefer water temperatures in the 16 to 20°C range. Temperatures in parts of the present Sacramento-San Joaquin Delta may be too warm for Sacramento perch during summer months (Woodley 2007). Potential changes to the Delta (e.g. island flooding) may improve conditions (Moyle 2008) for them but this needs to be determined.

Hypothesis 15: Physiological responses of larval and juvenile perch to the combined effects of unfavorable salinity, dissolved oxygen, and temperature determine survival rates. Multiple environmental factors affect the physiological responses of Sacramento perch. It is likely that if one factor is optimal, but others are not, perch may have low survival or reduced growth rates.

SAN FRANCISCO ESTUARY & WATERSHED SCIENCE

Hypothesis 16: Sacramento perch are able to maintain growth and reproduction in elevated salinities because of ion-regulation abilities. There is some indication that the perch could live in much of the San Francisco Estuary, suggesting that, like split-tail, they are euryhaline and presumably migrated to freshwater areas for spawning. If this is true, they may be able to be re-introduced into brackish waters.

Hypothesis 17: Contaminants (mercury, selenium, pesticides) in the Sacramento–San Joaquin system have a major effect on the reproduction, growth, and early life history of Sacramento perch. Laboratory studies of other fishes suggest that contaminants can be major limiting factors, but they affect survival is not known.

Genetics

Hypothesis 18: Low genetic diversity limits the viability of introduced populations of Sacramento perch. All perch populations today are introduced. Many of the introductions were made with limited numbers of fish radiating out from one initial introduction. Lake Greenhaven and the Elk Grove fish hatchery were the most common source for these initial introductions. How this low genetic diversity affects population viability is not known.

Hypothesis 19: Reintroduced populations established from more than one source exhibit better reproductive success. Genetic studies suggest existing populations come from diverse sources and so have different genetic make-ups. A strategy for taking advantage of this diversity needs to be developed.

Other Limiting Factors

Hypothesis 20: Sacramento perch are unable to maintain swimming velocities necessary to avoid water diversions and pumps. Studies by Woodley (2007) suggest that higher temperatures decrease the ability of perch to swim fast enough to avoid being entrained. The perch's ability to swim for extended periods must be investigated further.

Hypothesis 21: Sacramento perch are exceptionally vulnerable to disease, especially at warmer tempera-

tures. When adult perch were acclimated to 24 °C in experimental conditions they broke out in herpes-like rashes and were highly susceptible to gill parasites. How disease limits Sacramento perch populations is poorly understood, especially diseases from alien fishes.

DISCUSSION

Our analysis shows that the long-term decline of Sacramento perch is continuing. The species has generally been assumed to be in no danger of extinction because of the presence of multiple populations outside its native range. There are 28 known perch populations today, all isolated from one another. Sacramento perch were introduced into these waters because of its reputation as a game fish that could thrive in waters too alkaline to support other species of game fish. Despite the extraordinary physiological tolerances of the perch, these non-native waters represent sub-optimal conditions for it. The historic record indicates that the isolated, often stressed populations gradually become extirpated from these waters. The future of Sacramento perch is now precarious because no population can be regarded as truly secure. The perch may face severe genetic and demographic limitations.

In many ways, Sacramento perch are like other California-native freshwater fish species in their habitat requirements. The most striking of the habitat requirements is the need for cool water (<20 °C) for adults, reflecting evolution in riverine environments. In general, if water temperatures are optimal, Sacramento perch can persist in waters with high pH, low DO, and high salinity. If temperatures are too warm, their ability to thrive in poor water quality is decreased and growth rates and, presumably, survival declines. However, this ability, no doubt, allowed them to persist under adverse conditions in lakes, sloughs, and estuaries through periods of drought that are characteristic of Central California.

Their diet also reflects adaptability to changing conditions. It is varied and differs with the size of the fish and the availability of food by season. The diet of larval and early juvenile fish changes with the increase in gape as they grow (Crain and others

2007). Under optimal conditions, small perch first feed on aquatic invertebrates, especially abundant insect larvae, but then switch to fish as they grow larger. Growth rates, however, vary in response to population density, diet, gender, water temperature, anthropogenic influences, and alien species.

Sacramento perch generally start breeding during their second or third year of life.

They spawn at different times of the year in different bodies of water, with water temperature being the primary spawning cue that drives these differences. Survival of larvae is dramatically increased if water temperatures are cooler (15 to 22 °C), reflecting adaptation to spring spawning, when large productive littoral areas are likely to be flooded. Sacramento perch juveniles have greater ability to withstand high temperatures than adults, so they are able to use littoral areas and their more abundant food resources well into summer, thereby, avoiding predators in the process. In this respect, they are also like other native fishes.

Although they are usually compared in their adaptations to other centrarchid fishes, Sacramento perch differ from them in many ways. Swimming ability, for example, is higher than in other centrarchids with similar body morphology; this ability increases with size up to young adulthood, then decreases as they grow larger. This suggests adaptation for a life in large variable rivers, including backwater habitats for juveniles as indicated above. Males guard the nest quite vigorously, but apparently for shorter periods of time, and less aggressively than do other species of centrarchid. This behavior is perhaps a reflection of the perch's evolution in the absence of species with similar spawning behavior.

Although they can persist in adverse physical and chemical conditions and have adapted to local environmental conditions, Sacramento perch are severely limited by biotic interactions with alien species, especially other sunfish. In laboratory tests with bluegill, large perch were even less aggressive than small bluegill. Predation of early life history stages of perch by bluegill and other fishes may be the major source of mortality. Disease, perhaps brought in by non-native fishes, could also be a major limiting factor in

warm waters. In laboratory experiments, Sacramento perch were extremely vulnerable to disease and common parasites in waters over 18 °C. This suggests that extirpation from their native range was largely the result of the combination of massive habitat change, including diversion of cool water, and establishment of alien species, especially other centrarchids.

The information presented in this paper shows that restoration strategies for Sacramento perch will have to take into account the long isolation of the species from other centrarchids, and its specific adaptations to historic central California environments. A particular problem will be restoring the genetic diversity needed for long-term survival. Genetic diversity has suffered from low numbers of fish used to start populations and a lack of gene flow among populations. Genetic management will have to be part of any restoration plan, presumably by interbreeding fish from multiple locations. However, small initial population sizes and random fluctuations in allele frequencies, combined with unique ecological pressures associated with isolated locations where existing populations of Sacramento perch persist, pose the potential for lower fitness if fish from multiple sites are interbred at reintroduction sites (e.g., Fischer and Matthies 1997; Gharrett and others 1999; Schwartz and May 2008). Two populations are clearly preferred sources for reintroduction: Abbotts Lagoon and Clear Lake Reservoir. These populations had the highest number of alleles and the largest effective population sizes, as well as the greater number of unique alleles. However, these populations do not contain the entire genetic diversity of the species, making it necessary to draw from other populations to retain diversity at reintroduction sites.

All this suggests that the long-term persistence of Sacramento perch will require continual intervention by humans, especially if populations are to be re-established in the perch's native range. A carefully monitored breeding program will be required, along with major habitat restoration programs.

CONCLUSIONS

The following conclusions should be taken into account in the development of a Sacramento perch conservation program.

SAN FRANCISCO ESTUARY & WATERSHED SCIENCE

1. Sacramento perch have been extirpated from natural habitats in their native range, and many populations established outside the native range have disappeared. This indicates that the long-term decline of Sacramento perch is continuing, and that populations outside the native range cannot be depended on for persistence. By most definitions, the Sacramento perch is a Threatened or Endangered species.
2. Sacramento perch are extremely resistant to most environmental conditions as adults, but successful completion of life history requires cool water refuges and diverse habitat conditions.
3. Sacramento perch have diverged from other centrarchids in many respects, including: (a) their high fecundity, (b) their less elaborate reproductive behavior, and (c) their ability to withstand alkaline/saline water.
4. The optimal environment for Sacramento perch appears to be cool riverine habitat, with flooded areas available for spawning. They can survive in extreme environments (high temperatures, alkalinities, etc.) but they will eventually die out through a combination of poor growth, survival, and reproduction if such habitat is all that is available to them.
5. Almost all Sacramento perch today live in human-maintained habitats, mainly reservoirs and ponds, which are not suitable for their long-term survival.
6. Most, but not all, populations of Sacramento perch show signs of genetic bottle-necking (limited genetic diversity), but different populations have different genetic composition.
7. The presence of non-native centrarchids, especially sunfish (*Lepomis*) and crappie (*Pomoxis*), in Sacramento perch habitat is usually associated with their absence, although the exact mechanism of displacement is not fully understood.
8. Sacramento perch seem to be exceptionally vulnerable to disease, especially at warmer temperatures. This could be a result of low genetic heterogeneity due to inbreeding and founder effects, or from the presence of disease organisms.

9. The long-term trajectory for Sacramento perch in all its scattered populations combined is toward increasingly low genetic diversity, the gradual disappearance of populations in isolated ponds and reservoirs, and species extinction.
10. Sacramento perch have repeatedly proven to be a highly desirable food and sport fish, so recovery of fisheries for them should be the goal of long-term management.

MANAGEMENT

Any strategy for re-establishing Sacramento perch must take multiple factors into account. We propose the following as an 11-point conservation strategy, in no particular order of priority.

1. Ensure the future of all existing populations by establishing back-up populations from each source, including those outside of California. Ideally, these would be habitats within the native range of Sacramento perch, but managed ponds or lakes will also be necessary.
2. Establish a genetic management plan and program that brings the genotypes together from isolated populations to re-establish a genetically diverse source population for future planting programs. This would have to be done in a carefully controlled program with genetic monitoring of the fish produced as a source stock.
3. Establish a Sacramento perch rearing facility in the Central Valley, with facilities for selective breeding, and ponds for large-scale rearing of fish for planting, where populations should be established. Realistically, it may be necessary to maintain this facility indefinitely as a source of Sacramento perch to stock recreational ponds and reservoirs and as an insurance policy for wild populations.
4. Re-introduce fish into habitats that seem to be suitable in terms of other species' presence or absence and environmental conditions. Our physiological and ecological studies suggest that there are habitats from which Sacramento perch were extirpated decades ago that have changed enough

so that they may once again be suitable for them. Some of these habitats include:

Suisun Marsh. Sacramento perch have already been introduced (2006) into a pond at the Blacklock restoration site, but the success of this introduction is not known. We think there may be opportunities to re-introduce perch into some of the more natural tidal sloughs in the marsh, but this will require large numbers of fish and some careful evaluation of the potentially suitable sites (e.g., Mallard Slough 1 and 2).

Putah Creek, Solano Reservoir. This is a shallow, weedy run-of-river reservoir into which several hundred perch were introduced in 2005. We have found no sign of their presence since, however.

Wood Duck Slough, Cosumnes River Preserve. This slough has a small dam with a tidal gate across it. Sampling in 2004 indicated that other fishes were relatively scarce in the upper slough, so 700+ Sacramento perch were planted there in 2005. Re-sampling 6 months later showed that the slough had been massively invaded by other centrarchids, and no Sacramento perch were found. A single Sacramento perch of the right size was caught in Snodgrass Slough in September of 2008 by a CDFG crew. It is most likely that this perch originated from the 2005 planting. Presumably sloughs like this could be modified for successful perch introductions.

Barker Slough and Liberty Island Region, Solano County. This freshwater tidal area is likely to be the focus of habitat restoration for native fishes, especially Chinook salmon and splittail, for the Delta region. Sacramento perch should be incorporated into restoration plans.

San Luis Reservoir. This large reservoir apparently contains a small population of Sacramento perch but it has not been studied. It is not a natural habitat but may contain clues as to what conditions are needed to sustain Sacramento perch.

5. Develop a strategy to build/use floodplain ponds that will allow Sacramento perch to become distributed into natural environments during periods of flooding. A successful reintroduction will require a fairly large number of fish stocked and this is one way to achieve that. This strategy would take advantage of our previous studies of restoration of flooded habitat on the McCormick-Williamson Tract (CALFED project #99-B193) and the Cosumnes River Floodplain (CALFED Project #99-N06) (Crain and others 2003; Moyle and others 2007). There may also be potential for using ponds developed in gravel and sand mining operations for this purpose. This strategy should be linked to a more general strategy to develop flow regimes and habitats below dams that are generally more favorable to native fishes.
6. Develop a source-sink strategy by locating rearing ponds next to streams or sloughs so the ponds can 'leak' Sacramento perch on a regular basis into natural habitats. We have had success in developing populations of Sacramento perch in ponds on the UC Davis campus and have observed that small numbers have ended up in Putah Creek via drainage canals.
7. Rear Sacramento perch in large numbers in ponds and other artificial situations for large-scale introduction into the wild. This is the least desirable of the options we have been considering but may be necessary if information indicates that a large introduction size is necessary for re-establishment in the wild. This strategy may be especially important for trying to re-establish or maintain Sacramento perch populations in Clear Lake, Lake County, historically one of the last hold-outs of wild Sacramento perch in their native range.
8. Conduct a thorough search of Clear Lake (Lake County) using trawls, traps and large seines to see if any Sacramento perch remain. Bring fish captured into captivity so they can be propagated.
9. Develop and maintain an annual monitoring program for all known Sacramento perch populations in California. We have observed (e.g., in Lagoon Valley Reservoir) that large Sacramento

perch populations existing for long periods of time can become extirpated in 3 to 4 years. Monitoring will be essential to determine which populations are maintaining themselves, which ones are not, and why. Wild populations should be genetically monitored regularly.

10. Promote the use of Sacramento perch in recreational fisheries, especially farm ponds and city fishing programs. Their recreational and culinary properties are currently under-appreciated, and a program like this would not only acquaint people with an edible native sport fish but increase the likelihood of Sacramento perch being maintained in private ponds and of their escaping to the wild.
11. Give the Sacramento perch special status to emphasize the urgency of its recovery. It is currently a Species of Special Concern in California and could qualify as a state or federal Threatened (or even Endangered) species. It was included as a component of the Delta Native Fishes Recovery Plan (USFWS 1996), but nothing has been done with this. More research on this fish is needed, but its need for conservation is already well justified.

ACKNOWLEDGMENTS

This research was conducted as part of a cooperative research venture managed by the Watershed Sciences Center (WSC) at the University of California, Davis. Jeffrey Mount, Director of the Center, made our lives easier by running the Center's programs so well. We thank Dr. Christa Woodley and Dr. Rachel Schwartz for sharing information and insights from their dissertation work with us, as well as their dissertation advisors, Dr. Joseph Cech and Dr. Bernie May for providing additional insights into the worlds of genetics and physiology. Chris Miller of the Contra Costa County Vector Control Agency shared information and insights from his Sacramento perch rearing program. We thank Ellen Mantalica and Diana Cummings for their help on the often complex budget and management issues of the project. This project was funded by the CALFED Bay-Delta Authority (CALFED, Project # ERP-02-P34).

REFERENCES

- Aceituno ME, Nicola SJ. 1976. Distribution and status of the Sacramento perch *Archoplites interruptus* in California. *California Fish and Game* 62:246–254.
- Aceituno ME, Vanicek CD. 1976. Life history studies of the Sacramento perch *Archoplites interruptus* in California. *California Fish and Game* 62:5–20.
- Aguilar A, Jones J. 2009. Nuclear and mitochondrial diversification in two native California minnows: insights into taxonomic identity and regional phylogeography. *Molecular Phylogenetics and Evolution* 51(2):373–381.
- Bacon ME. 1980. An ethological study of the Sacramento perch *Archoplites interruptus* and its interaction with bluegill *Lepomis macrochirus* [M.S. thesis]. Sacramento (CA): California State University. 49 p.
- Bliesner KL. 2005. Trophic ecology and bioenergetics modeling of Sacramento perch (*Archoplites interruptus*) in Abbots Lagoon, Point Reyes National Seashore [M.S. thesis]. Arcata (CA): Humboldt State University. 82 p.
- Broughton JM. 1994. Late Holocene resource intensification in the Sacramento Valley, California: the vertebrate evidence. *Journal Archaeological Science* 21:501–514.
- Carlander KD. 1977. The handbook of freshwater fishery biology. Vol. II. Ames (IA): Iowa State University Press. 431 p.
- [CDFG] California Department of Fish and Game. 1996. Memo from Fred Meyer to Nick Villa regarding electrofishing results for Lagoon Valley Reservoir [dated April 23, 1996].
- [CDFG] California Department of Fish and Game. 2008. State inland angling records. [Internet; updated 2009 May 27]. Sacramento (CA): California Department of Fish and Game. [cited 2009 Jun 3]. Available from: <http://nrm.dfg.ca.gov/AnglingRecords/Default.aspx>

- [CDWR] California Department of Water Resources. 1995. Sacramento San-Joaquin Delta Atlas. State of California, Department of Water Resources, Sacramento, California. 121 p.
- Coleman GA. 1930. A biological survey of Clear Lake, Lake County. California Fish Game 15:221-227.
- Cook SF Jr., Moore RL, Connors JD. 1966. The status of the native fishes of Clear Lake, Lake County, California. Wassmann Journal of Biology 24:141-160.
- Cook SJ, Philipp DP, Wahl DH, Weatherhead PJ. 2006. Energetics of parental care in six syntopic centrarchid fishes. Oecologia 148:235-249.
- Cooper JJ. 1978. Contributions to the life history of the Lahontan tui chub (*Gila bicolor*) in Walker Lake, Nevada [M.S. thesis]. Reno (NV): University of Nevada, Reno. 98 p.
- Cooper JJ, Koch DL. 1984. Limnology of a desertic terminal lake, Walker Lake, Nevada, USA. Hydrobiologia 118:275-292.
- Crain PK, Corcoran DM. 2000. Age and growth of tui chub in Eagle Lake, California. California Fish and Game 86:149-155.
- Crain PK, Small KM, Moyle PB. 2003. Survey of fish and their diets surrounding the McCormack-Williamson Tract (2001-2002). Final report. CALFED project #99-B193. 34 p.
- Crain PK, Woodley CM, Schwartz RS, Moyle PB, May B. 2007. Restoration of the Sacramento perch to the San Francisco Estuary. Final report, CALFED Project #ERP-02-P34. 47 p.
- Curtis B. 1949. The warm-water game fishes of California. California Fish and Game 35:255-274.
- Dill WA, Cordone AJ. 1997. History and status of introduced fishes in California, 1871-1996. California Department of Fish and Game Fish Bulletin 178. Sacramento (CA): Department of Fish and Game. 414 p.
- Falter MA, Cech JJ. 1991. Maximum pH tolerance of three Klamath Basin fishes. Copeia 1991:1109-1111.
- Fischer M, Matthies D. 1997. Mating structure and inbreeding and outbreeding depression in the rare plant *Gentianella germanica* (*Gentianaceae*). American Journal of Botany 84:1685-1692.
- Fong S, Takagi T. 1979. Competition among four centrarchids in Clear Lake, Lake County, California. Unpublished report. Available from: University of California, Davis. 41 p.
- Fuller P. 2009. *Archoplites interruptus*. USGS nonindigenous aquatic species database [Internet]. Gainesville (FL): USGS. Available from: <http://nas.er.usgs.gov/queries/FactSheet.asp?speciesID=374> > Revision Date: 4/11/2006.
- Galat DL, Lider EL, Vigg S, Robinson SR. 1981. Limnology of a large, deep, North American terminal lake, Pyramid Lake, Nevada, U.S.A. Hydrobiologia 42: 281-317.
- Gharrett AJ, Smoker WW, Reisenbichler RR, Taylor SG. 1999. Outbreeding depression in hybrids between odd and even brood year pink salmon. Aquaculture 173:117-129.
- Gill TN. 1861. Notes on some genera of fishes of the western coast of North America. Philadelphia (PA): USA Proceedings, Academy of Natural Sciences. 13:164-168.
- Girard C. 1854. Descriptions of new fishes, collected by Dr. A L. Heerman, naturalist attached to the survey of the Pacific Railroad Route, under Lieut. R. S. Williamson. Philadelphia (PA): USA Proceedings, Academy of Natural Sciences. 7:129-140.
- Gobalet KW. 1989. Remains of tiny fish from a late prehistoric Pomo site near Clear Lake, California. Journal California and Great Basin Anthropology 11:231-239.
- Gobalet KW. 1990. Prehistoric status of freshwater fishes of the Pajaro-Salinas River system of California. Copeia 1990:680-685.
- Gobalet KW. 1993. Additional archaeological evidence for endemic fishes of California's Central Valley in the coastal Pajaro-Salinas basin. The Southwestern Naturalist 38:218-223.

SAN FRANCISCO ESTUARY & WATERSHED SCIENCE

- Goode GB. 1884. The fisheries and fishery industries of the United States. Washington D.C.: United States Commission of Fish and Fisheries. 895 p.
- Grosholz E, Gallo E. 2006. The influence of flood cycle and fish predation on invertebrate production on a restored California floodplain. *Hydrobiologia* 568(1):91-109.
- Hess L, Karp C, Wang J. 1995. Sacramento perch, wakasagi, splittail, Sacramento blackfish, and shimofuri goby in San Luis reservoir and O'Neill Forebay. IEP Newsletter. Sacramento (CA): Department of Water Resources. Available from: <http://www.water.ca.gov/iep/products/newsletterPrevious.cfm>.
- Holliday JS. 1999. Rush for riches: Gold fever and the making of California. Berkeley (CA): UC Press.
- Hopkirk JD. 1973. Endemism in fishes of the Clear Lake Region. University of California Publications in Zoology 96. 160 p.
- Hrabik RA. 1989. Fishes. In: Bleed A, Flowerday C, editors. An atlas the Sand Hills. Resource atlas number 5/1989. Reprinted 2005. Lincoln (NA): University of Nebraska, Lincoln, Conservation and Survey Division. p. 143-154.
- Hubbs C. 1947. Mixture of marine and freshwater fishes in the lower Salinas River, California. *Copeia* 1947:147-149.
- Imler RL, Weber DT, Fyock OI. 1975. Survival, reproduction, age, growth, and food habits of Sacramento perch *Archoplites interruptus* (Girard), in Colorado. *Transactions of the American Fisheries Society* 104:232-236.
- Jeffres CA, Opperman JJ, Moyle PB. 2008. Ephemeral floodplain habitats provide best growth conditions for juvenile Chinook salmon in a California river. *Environmental Biology of Fishes* 83:449-458.
- Jelks HL, Walsh SJ, Burkhead NM, Contreras-Balderas S, Díaz-Pardo E, Hendrickson DA, Lyons J, Mandrak NE, McCormick F, Nelson JS, Platania SP, Porter BA, Renaud CB, Schmitter-Soto JJ, Taylor EB, Warren ML Jr. 2008. Conservation status of imperiled North American freshwater and diadromous fishes. *Fisheries* 33:372-407.
- Jellison R, Rose K, Melack JM. 2003. Assessment of internal nutrient loading to Crowley Lake, Mono County. Report to State Water Resources Control Board #00-196-160-0.
- Jordan DS, Evermann BW. 1896. Fishes of North and Middle America. *Bulletin U.S. National Museum* 47(1-4):1-3705.
- Jordan DS, Evermann BW. 1923. American food and game fishes. New York: Doubleday. 572 p.
- Jordan DS, Gilbert CH. 1886. Synopsis of the fishes of North America. *Bulletin U.S. National Museum* 16:1-1018.
- Jordan DS, Gilbert CH. 1894. List of the fishers inhabiting Clear Lake, California. *Bulletin of the United States Fish Commission* XIV p. 139-140.
- Knight NJ. 1985. Microhabitats and temperature requirements of hardhead (*Mylopharodon conocephalus*) and Sacramento squawfish (*Phytochocheilus grandis*), with notes for other native California stream fishes [Ph.D. Dissertation]. Davis (CA): University of California, Davis. 161p.
- La Rivers I. 1962. Fishes and fisheries of Nevada. Nevada State Fish and Game Comm. 782 p.
- Leon A, Miller CE, Tey SJ. 2008. Early development of the Sacramento perch. *North American Journal of Aquaculture* 70:27-37.
- Linden A, Cech JJ Jr. 1990. Prey selection by mosquitofish (*Gambusia affinis*) in California rice fields: effect of vegetation and prey species. *Journal of the American Mosquito Control Association* 6:115-120.
- Marchetti MP. 1999. An experimental study of competition between native Sacramento perch *Archoplites interruptus* and introduced bluegill *Lepomis macrochirus*. *Invasion Biology* 1:55-65.
- Mathews SB. 1962. The ecology of the Sacramento perch, *Archoplites interruptus*, from selected areas of California and Nevada [M.A. thesis]. Berkeley (CA): University of California, Berkeley. 93 p.
- Mathews SB. 1965. Reproductive behavior of the Sacramento perch, *Archoplites interruptus*. *Copeia* 1965:224-228.

- Maybe PM. 1993. Phylogenetic interpretation of ontogenetic change: sorting out the actual and artefactual in an empirical case study of centrarchid fishes. *Zoological Journal of the Linnean Society* 107:175-291.
- McCarragher DB, Gregory RW. 1970. Adaptability and current status of introductions of Sacramento perch, *Archoplites interruptus*, in North America. *Transactions of the American Fish Society* 100:700-707.
- Miller C. 2003. Embryonic development of the Sacramento perch, *Archoplites interruptus*: A preliminary [unpublished] report. Concord (CA): Mosquito and Vector Control Division, Contra Costa County.
- Miller C. 2004. 2004 Annual report, fisheries section [unpublished report]. Concord (CA): Mosquito and Vector Control Division, Contra Costa County.
- Miller RR, Alcorn JR. 1943. The introduced fishes of Nevada, with a history of their introduction. *Transactions of the American Fish Society* 73:175-193.
- Minckley WL. 1973. Fishes of Arizona. Phoenix (AZ): Arizona Department of Fish and Game.
- Moyle PB. 1976. Inland fishes of California. Berkeley (CA): University of California Press. 405 p.
- Moyle PB. 2002. Inland fishes of California, revised and expanded. Berkeley (CA): University of California Press. 502 p.
- Moyle PB. 2008. The future of fish in response to large-scale change in the San Francisco Estuary, California. In: McLaughlin KD, editor. Mitigating impacts of natural hazards on fishery ecosystems. Bethesda (MD): American Fishery Society, Symposium 64. p 357-374.
- Moyle PB, Baxter RD, Sommer T, Foin TC, Matern SA. 2004. Biology and population dynamics of Sacramento splittail (*Pogonichthys macrolepidotus*) in the San Francisco Estuary: a review. *San Francisco Estuary and Watershed Science* [Internet]. Available from: <http://www.escholarship.org/uc/item/61r48686>
- Moyle PB, Light T. 1996. Biological invasions of fresh water: empirical rules and assembly theory. *Biological Conservation* 78:149-161.
- Moyle PB, Mathews SB, Bonderson N. 1974. Feeding habits of the Sacramento perch, *Archoplites interruptus*. *Transactions of the American Fish Society* 103:399-402.
- Moyle PB, Pine R, Brown LR, Hanson CH, Herbold B, Lentz KM, Meng L, Smith JJ, Sweetnam DA, Winternitz L. 1996. Recovery plan for the Sacramento-San Joaquin Delta native fishes. Portland (OR): U.S. Fish and Wildlife Service. 193 p.
- Moyle PB, Yoshiyama RM, Williams JE, Wikramanayake ED. 1995. Fish species of special concern of California. 2nd ed. Sacramento (CA): Department of Fish and Game.
- Murphy GI. 1948. A contribution to the life history of the Sacramento perch (*Archoplites interruptus*) in Clear Lake, Lake County, California. *California Fish and Game* 34:93-100.
- Neale G. 1931. Spiny-rayed fresh water game fishes of California inland waters. *California Fish and Game* 17:1-16.
- Near TJ, Bolnick DI, Wainwright PC. 2004. Investigating phylogenetic relationships of sunfishes and black basses (*Actinopterygii: Centrarchidae*) using DNA sequences from mitochondrial and nuclear genes. *Molecular Phylogenetic Evolution* 32:344-357.
- Near TJ, Bolnick DI, Wainwright PC. 2005. Fossil calibrations and molecular divergence time estimates in centrarchid fishes (*Teleostei: Centrarchidae*). *Evolution* 59:1768-1782.
- Parker HG. 1879 First biennial report of the fish commissioner of the State of Nevada, 1877-1878. p. 1-7.
- Parker HG. 1881. Biennial report of the Fish Commissioner of the state of Nevada, 1879-1880. p. 1-10.
- Pintler HE, Johnson WC. 1958. Chemical control of rough fish in the Russian River drainage, California. *California Fish and Game* 69:124-128.

- Reid SB, Cowan W, Beyers S. 2003. Mainstream upper Pit River fish surveys, including the North and South Fork Pit rivers September 2002. Report to U.S. Fish and Wildlife Service. Klamath Falls (OR): U.S. Fish and Wildlife Service. 38 p.
- Ribeiro F, Crain PK, Moyle PB. 2004. Variation and condition factor and growth in young-of-year fishes in floodplain and riverine habitats of the Cosumnes River, CA. *Hydrobiologia* 527:77–84.
- Ridgway MS, Shuter BJ, Post EE. 1991. The relative influence of body size and territorial behaviour on nesting asynchrony in male smallmouth bass, *Micropterus dolomieu* (Pisces: Centrarchidae). *Journal of Animal Ecology* 60:665–681.
- Rutter C. 1908. The fishes of the Sacramento–San Joaquin basin, with a study of their distribution and variation. *Bulletin U.S. Bureau of Fisheries* 27:103–152.
- Saiki MK, Martin BA. 2001. Survey of fishes and environmental conditions in Abbotts Lagoon, Point Reyes National Seashore, California. *California Fish and Game* 87:123–138.
- Schulz PD, Simons, D.D. 1973. Fish species diversity in a prehistoric central California Indian midden. *California Fish and Game* 59:107–113.
- Schwartz RS, May B. 2004. Characterization of microsatellite loci in Sacramento perch (*Archoplites interruptus*). *Molecular Ecology Notes* 4:694–697.
- Schwartz R, May B. 2008. Genetic evaluation of isolated populations for use in reintroductions reveals significant genetic bottlenecks in potential stocks of Sacramento perch. *Transactions of the American Fish Society* 137:1764–1777.
- Sigler WF, Sigler JW. 1987. *Fishes of the Great Basin: a natural history*. Reno (NV): University of Nevada Press. 425 p.
- Skinner JE. 1962. An historical view of the fish and wildlife resources of the San Francisco Bay Area. CDFG Water Projects Branch Report 1. 225 p.
- Snyder JO. 1913. The fishes of the streams tributary to Monterey Bay, California. *Bulletin of the U.S. Bureau of Fisheries* 32:49–72.
- Sommer TR, Nobriga ML, Harrell WC, Batham W, Kimmerer WJ. 2001. Floodplain rearing of juvenile Chinook salmon: evidence of enhanced growth and survival. *Canadian Journal of Fisheries and Aquatic Sciences* 58:325–333.
- Sublette JE, Hatch MD, Sublette M. 1990. *The fishes of New Mexico*. Albuquerque (NM): University of New Mexico Press. 393 p.
- Turner JL. 1966. Distribution and food habits of centrarchid fishes in the Sacramento–San Joaquin Delta. In: Turner JL, Kelley DW, editors. *Ecological studies of the Sacramento–San Joaquin Delta. Part II. Fishes of the Delta*. California Department of Fish and Game Fish Bulletin 136. Sacramento (CA): California Dept. of Fish and Game. p. 144–153.
- Vanicek DC. 1980. Decline of the Lake Greenhaven Sacramento perch population. *California Fish and Game* 66:178–183.
- Vigg S. 1978. Vertical distribution of adult fish in Pyramid Lake, Nevada. *Great Basin Naturalist* 38:417–428.
- Vigg S, Kucera P. 1981. Contributions to the life history of Sacramento perch, *Archoplites interruptus*, in Pyramid Lake, Nevada. *Great Basin Naturalist* 41:278–289.
- Vinyard GL. 1980. Differential prey vulnerability and predator selectivity: effects of evasive prey on bluegill *Lepomis macrochirus* and pumpkinseed *L. gibbosus* predation. *Canadian Journal of Fisheries and Aquatic Sciences* 37:2294–2299.
- Vinyard GL. 1982. Variable kinematics of Sacramento perch *Archoplites interruptus* capturing evasive and nonevasive prey. *Canadian Journal of Fisheries and Aquatic Sciences* 39:208–211.
- Walford LA. 1931. *Handbook of common commercial and game fishes of California*. Division of Fish and Game of California. Fish Bulletin 28. Sacramento (CA): State Printing Office. 183 p.

Wang JCS. 1986. Fishes of the Sacramento–San Joaquin Estuary and adjacent waters, California: a guide to their early life histories. California Department of Water Resources, Interagency Ecological Program, Technical Report 9, Sacramento (CA): California Dept. of Water Resources. 800 p.

Wang JCS, Reyes RC. 2008. Early life stages and life histories of Centrarchids in the Sacramento–San Joaquin River Delta System, California. Tracy Fish Collection Facility Studies. Vol. 42. U.S. Bureau of Reclamation, Mid Pacific Region, and Denver Technical Service Center. 104 p.

Webb PW. 1975. Acceleration performance of rainbow trout *Salmo gairdneri* and green sunfish *Lepomis cyanellus*. J. Experimental Biology 63:451–465.

Woodley CM. 2007. Using ecological physiology for the conservation and restoration of a declining species: a case study Sacramento perch (*Archoplites interruptus*) [Ph.D. dissertation]. Available from: University of California, Davis. 165 p.