TROUT UNLIMITED OF CALIFORNIA LAUNCHES MAJOR EFFORT TO SAVE THREATENED TROUT

Trout Unlimited members throughout California gathered forces for a summer 1986 project to help save a threatened subspecies of wild trout: the Paiute cutthroat *(Salmo clarki seleniris)*. The project took place in two phases, the first during the Fourth of July weekend and the second during the Labor Day weekend.

The focus of the volunteer conservationists is restoration of critical stream habitat in the upper reaches of Silver King Creek in the Sierra Nevada Mountains. Silver King is in east-central California within Toiyabe National Forest. The TU effort was a cooperative project with the United States Forest Service and the California Department of Fish and Game.

The Paiute cutthroat is a rare, distinct subspecies that has evolved in isolation from other fishes. The subspecies can be distinguished from other cutthroats by the absence—or near-absence—of body spots. Its body coloration is typically coppery to purplish-pink. In 1970 the United States Fish and Wildlife Service officially listed the Paiute cutthroat as an endangered species; in 1975 it was reclassified as threatened. It is estimated that no more than 500 adults remain alive.

In the early 1900s the Paiute cutthroat was eliminated from its historic habitat by hybridization with both rainbow trout and Lahontan cutthroat trout. Two small populations of genetically pure Paiute cutthroat are known to exist in Silver King Creek.

Many problems threaten the continued existence of the Paiute due to its limited distribution. Habitat degradation is severe in the Silver King drainage. Beavers, introduced in the early 1900s, removed the original willow and aspen growth along the creek and its tributaries. The dams created by these rodents seriously degraded habitat by contributing to siltation. Trampling by domestic livestock in the Silver King basin has retarded the regrowth of willows and aspen along the streambank. Livestock overgrazing has further contributed to the sloughing of overhanging banks. This results in loss of cover, higher water temperatures, loss of spawning habitat, and loss of food sources.

Volunteers construct a bank stabilization structure on California's Silver King Creek.

A comprehensive recovery plan was prepared by fisheries biologist Edward M. Lorentzen of the United States Fish and Wildlife Service. The goals of the plan are: (1) Reestablish a pure population of Paiute cutthroat in Silver King Creek above Llewellyn Falls; and (2) Secure and maintain the integrity of the habitat over a consecutive five-year period to insure stable or increasing overwintering populations of at least 500 fish.

The first phase of the project took place on the Fourth of July weekend. More than 50 volunteers met at the pack station to begin the six- or eleven-mile trek to Silver King (the eleven-mile was the easiest). Pack trains were utilized to bring in food, tools, and other supplies.

The main thrust of this first phase was to install six miles of solar powered electric fences along portions of the stream bank. The fences will keep browsing cattle away from stream banks, allowing vegetation to recover. During the Fourth of July weekend the crews, using hand-operated cross-cut saws (chain saws are not allowed in wilderness areas), prepared lodgepole logs for bank stabilization structures to be installed during the Labor Day project.

On Labor Day weekend the troops once again assembled for an assault on Silver King. In a meadow set between towering peaks the work parties put their muscle to the task. Fallen trees were hauled 200 yards to the stream. Holes were dug to set anchor members to which the timbers were secured by steel reinforcing rods driven through the wood into the embankment. The finished structure was back-filled with rocks hand-carried to the site. Willow cuttings were planted around the completed structure to provide additional anchoring and cover for the trout.

Farther upstream, in two important spawning tributaries to Silver King, crews cleared debris that blocked spawning access, and in other sections added streamside cover.

The volunteers were from many walks of life and a variety of places, including a retired cook from San Francisco, a retired freight claims man from the Southern Pacific Railroad, two high school football players, and numerous husband-wife teams. All were bonded by a common goal—to preserve the habitat and future of the Paiute cutthroat trout.

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The Magazine for Trout and Salmon Anglers

Spring 1987 Volume 28 Number 2

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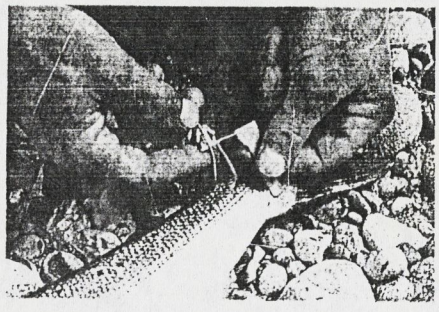

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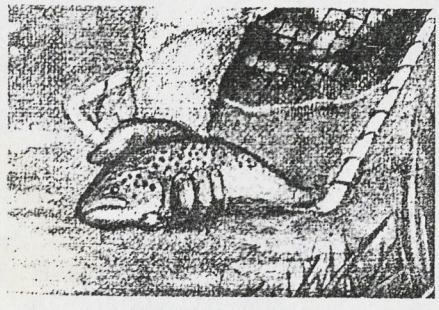

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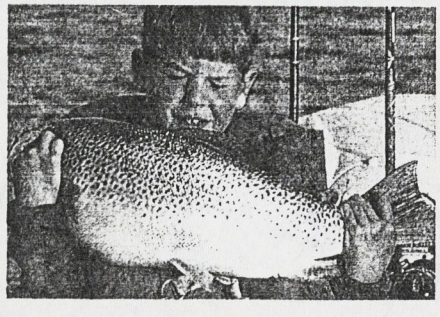

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Cover: A fresh-run Atlantic salmon grilse, once swimming in the Miramichi, now swimming in sour cream and dill. Photograph by Thomas R. Pero.

Center Painting: Paiute cutthroat trout by Lee Stroncek.

SIERRA CLUB

Toiyabe Chapter — Nevada and Eastern California
P.O. Box 8096, Reno, Nevada 89507

1/6/88

TOIYABE NATIONAL FOREST
CRISIS IN PUBLIC LAND MANAGEMENT

The Toiyabe Forest Plan, completed in 1986, has been hailed by resource professionals and conservationists as a long overdue commitment to improving unsatisfactory range management on national forests in Nevada. The Plan standards and guidelines, especially on forage utilization and riparian area management and protection, are being used as guides for forest plans all over the West. The Plan has been appealed by a group of central Nevada ranchers who fear that the good old days of Forest Service acquiescence to livestock overgrazing and mismanagement are about to end. The Nevada Cattlemens' Association and related groups are fundraising to finance the appeals. Not sure that the appeals process will be in their favor, these groups are attempting to bring political pressure on the Forest Service at state and national levels to influence the appeal and overturn the Plan.

Intervening on behalf of the Forest Service, the Nevada Department of Wildlife, the Toiyabe Chapter of the Sierra Club, the Nevada Wildlife Federation, Cal Trout, American Fisheries Society, the Izaac Walton League, Northern California Council Federation of Fly Fishers, and three individuals are strongly supporting the standards and guidelines in the Plan. Several of the intervenors have provided extensive documentation of poor range conditions and trends and the need for improved management. Now, the groups are trying to generate support for the Plan to counteract the Appellants politicking.

WHAT THE FIGHTING'S ALL ABOUT

A close look at the background of the problem shows why the Plan and Appeal have raised such controversy. The Toiyabe National Forest contains 3.2 million acres (1.1 suitable for grazing). According to Forest records, another 250,000 acres of unsuitable range is currently being grazed by livestock. According to Forest records, 40-45% of the Toiyabe rangelands are in poor condition, more than that of any other national forest. In the early '60's, when much of the rest of the Intermountain Forest Region was embroiled in the conflicts of making reductions in livestock and applying better grazing management, the Toiyabe was asked by its Regional office not to take controversial actions. Due to that request and the strong political clout of the Nevada ranchers, range management on the Toiyabe is 20 to 30 years behind most other forests. The typical grazing practices- spring turnout, heavy grazing on the same areas all season, and late fall removal - continue. Most permittees resist any management changes and strongly oppose any stocking reductions.

There have been some changes in management since the forest was created. But these have primarily been through shortening the season of use and some reduction in livestock numbers. Cattle use the canyon bottoms heavily until all of the streamside vegetation is gone. Then they move up onto the steeper sidehills. During the early part of the century, almost all of the range was in poor condition. Due to the shortened grazing seasons and reduced stocking, less use was made of areas away from the stream bottoms. These steeper areas have improved substantially since the early 1900's and are often used as examples of range improvement.

But since the cattle concentrate of the more level areas such as riparian zones, these areas are still in poor and declining condition. Some apologists for the livestock industry point out that there is more vegetation along the streams than there was 80 years ago. This may be true, but the current vegetation is not sufficient to prevent extensive ongoing soil erosion. Soil and productivity losses continue to occur. These losses are dramatic during exceptionally high runoff. Wayne Padgett, a Forest Service ecologist, says that the riparian aras of Central Nevada are the worst he has seen anywhere.

Changes in current grazing practices, such as rotation grazing and vegetation use levels that allow the recovery of more desirable plants, are needed. According to Barry Davis, of the Toiyabe National Forest, with proper management the riparian areas could produce three to four times more forage in as little as ten years. Current vegetation utilization is far in excess of 80% in many allotments. Most research shows that utilization over 60% is very deleterious to riparian habitat. The Forest Plan prescribes a maximum of 65% when the riparian areas are in satisfactory condition and 55% when they are in unsatisfactory condition. These are maximum amounts of use and are probably too high, even for wet meadows. Some researchers believe that utilization should not exceed 35% on streambanks with fisheries even when included in a rest rotation system of grazing management. The actual levels are to be set by an interdisciplinary team when the Allotment Management Plans are written. These maximum utilization standards are the primary ones being appealed by the permittees. The appellants feel that the standards are too restrictive and should allow for more use.

The Forest has had success with good management systems when they can be applied. For example, a better system of management was initiated in 1970 on the Table Mountain allotment. The improvement has been dramatic, with all the range now in fair to excellent condition. In addition to supporting the original livestock numbers, the allotment now supports about 200 elk. The sage grouse population is strong and the trout fishery excellent.

Another demonstration allotment is the Bunker allotment in the center of the most overgrazed area in Central Nevada. The sheep are grazed using a system of management which rotates light use

over the allotment. The uplands are in good condition and the riparian aras are in good to excellent condition. While there was considerable soil lost from the stream channels on adjacent allotments during the floods of the early '80's, the streams within the Bunker allotment remained essentially intact. According to Bill Platts of the Intermountain Research Station, the Central Nevada streams are extremely productive and have the potential of increasing fish production by 3 to 5 times. Several of the hardest hit streams provide habitat for the threatened Lahontan cutthroat trout.

Conservationists and resource professionals are very pleased that the Forest Service is finally tackling the problem of improving range conditions. Through the Forest Plan, the Toiyabe is concentrating on the riparian areas, first. The strong belief is that when riparian areas are managed correctly, the remaining areas, for the most part, will also be managed correctly.

Most of the permittees who appealed the Plan did so because the Forest is implementing local plans to improve range conditions on their allotments. The appellants are Tony and Beulah Testolin, Jim Champie, LaVar Young, Wes and Mary Parsons, and Howard Wolf. From a range condition standpoint, their allotments are among the poorest on the Forest. Utilization has been heavy for many years with resulting decrease in plant diversity. The allotments involved are Bade Flat and Tierney. There have been several plans for these allotments, all of which the permittees have not followed. The permittees were also involved in the development of current allotment plans and have appealed these as well as the Forest Plan.

Conservationists have always felt that the Forest Service has afforded permittees more consideration in these on-the-ground plans than other public land interests. All permittees are extensively involved in designing their allotment management plans. Once the plan is approved and implemented, any significant adverse changes to the permittee are phased in over a period of years. For example, when stocking adjustments appear necessary, they are handled as follows: Each year studies are made to determine when proper use is reached. The first year the permittee is <u>encouraged</u> to leave early once proper use is reached. The second year the permittee is <u>asked to leave as soon as possible</u> once proper use is reached. Then finallly during the third year, the cattle <u>must leave</u> so that proper use is not exceeded.

The Forest appears to be bending over backward to cooperate with these permittees. Not only is the Toiyabe going through this three year process before reductiions are ordered, but it is offering the permittees alternatives including the use of excess forage on nearby allotments.

Instead of working to resolve the resource management problems, the permittees are employing an old strategy - attack the Forest

Service administrator who is trying to implement needed changes. Complaints like "we can't work with him," and "we weren't involved" abound. Unfortunately, this strategy may be working as the District Ranger and Range Conservationist have just been transferred to other Forests.

Less than one third of the Toiyabe's allotments are properly managed. According to the Forest Plan, during the next 8-10 years, five or six allotments per year will be placed under improved management. The resistance to changing present management will be considerable. Conservationists must win the fight over the Plan standards and guidelines and their implementation NOW or forever accept unsatisfactory management of our public lands.

HOW TO HELP:

* **WRITE** to government officials to not back down on the Toiyabe Forest Plan and appeal:

Richard E. Lyng, Secretary
US Department of Agriculture
Adm. Bldg. 12th & Jefferson, SW
Washington, DC 20250

Dale Robertson, Chief
US Forest Service
PO Box 2417
Washington, DC 20013

* **WRITE** to elected officials to support the Forest Plan and good range management on the Toiyabe National Forest:

Senator Chic Hecht
Senator Harry Reid
Senator Alan Cranston
Senatory Pete Wilson

Congr. James Bilbray
Congr. Barbara Vucanovich
Congr. Rick Lehman
Congr. Norm Shumway
Congr. Bill Thomas

The Honorable _____
US Senate
Washington, DC 20510

The Honorable _____
US House of Representatives
Washington, DC 20515

* **WRITE** a letter to the editor of your local newspaper, outlining the situation and urging others to write in support of the Toiyabe Forest Plan.

FOR MORE INFORMATION, CONTACT:

Rose Strickland, Toiyabe Chapter of the Sierra Club, PO Box 8096, Reno, NV 89507 or call (702) 329-6118.

Rep. Jim Bilbray
Representative
1431 Longworth House
Washington D.C. 20515

Sen. Chic Hecht
Senator
302 Senate Hart Bldg.
Washington D.C. 20510

Rep. Barbara Vucanovich
Representative
312 Cannon House Office Bld
Washington D.C. 20515

Senator Harry Reid
Senator
708 Senate Hart Building
Washington D.C. 20510

Mr. Richard E. Lyng
Secretary of Agriculture
Adm.Bld. 12th St & Jeff. SW
Washington D.C. 20250

Mr. Peter C. Myers
Assist. Sectetary of Agriculture
Adm.Bld. 12th St.& Jeff. SW
Washington D.C. 20250

Mr. Dale Robertson
Chief of the Forest Service
S.Bld. 12th & Independence
Washington D.C. 20250

Mr. Richard Bryan
Governor
Capitol Building
Carson City NV 89710

TOIYABE'S CURRENT RANGE SITUATION

The Toiyabe National Forest contains approximately 3.2 million acres of which about 1.1 is suitable for grazing. Approximately, an additional 250,000 acres of unsuitable range is currently being grazed by livestock. Forty to forty five percent of Toiyabe's rangelands are in poor condition. This is a higher percentage than that of any other national forest. In the early 1960's, when much of the rest of Region IV was embroiled in the conflict of making reductions in livestock and applying good management the Toiyabe was asked by its regional management to wait and not "stir the pot". Due to that request and the strong clout of Nevada ranchers, range management on the Toiyabe is 20 to 30 years behind the other forests. The predominate livestock management practice is to place the livestock on the forest in the spring, graze the same areas heavily all season, and remove the stock in the fall. Most permittees resist any management changes and strongly oppose any stocking reductions.

There have been some changes in management since the forest was created. But these have primarily been through shortening the season of use and some reductions in livestock numbers. Cattle use the bottoms heavily until all of the feed is gone. They will then move up on to the steeper side hills. During the early part of the century almost all of the range was in poor condition. As the grazing season was shortened and stocking reduced less and less use was made of the areas away from the stream bottoms. These steeper areas have improved substantially since the early 1900's and are often used as examples of range improvement. But since the cattle concentrate on the more level areas such as riparian zones, these areas are still in poor condition. In fact, their condition over most of the forest is declining. Some "experts" point out that there is more vegetation along the streams than there was 80 years ago, but the current vegetation is not sufficient to prevent accelerated soil losses. Soil and productivity losses are occurring. These losses are dramatic during exceptionally high runoff. Wayne Padgett, a Forest Service ecologist, says that the riparian areas of Central Nevada are the worst he has seen anywhere.

The grazing management needed is rotation grazing and vegetation use levels that allow the recovery of the more desirable plants. According to Barry Davis of the Toiyabe National Forest, with proper management the riparian areas could produce three to four times more forage in ten years. Current vegetation utilization is far in excess of 80 percent. Most research shows that utilization in excess of 60 percent is very deleterious to riparian habitat. The Forest Plan prescribes a maximum of 65 percent when the riparian areas are in satisfactory condition and 55 percent when they are in unsatisfactory condition. These are maximum amounts of use and are probably too high. A significant amount of research demonstrates that utilization should not exceed 35 percent even when included in a rest rotation system of management. The actual levels will be set by an interdisciplinary team when the Allotment Management Plan is written. These maximum utilization standards are the primary point being appealed in the grazing appeal of the Toiyabe's Forest Plan. The appellants feel that the standards are too restrictive and should allow for more use.

The forest has had success with good management systems when they can be applied. An example is the Table Mountain C&H allotment. In 1970, an improved

system of management was initiated on the allotment. At that time more than half of the allotment was in poor condition. Since then the improvement has been dramatic. All of the range is now in fair to excellent condition. The allotment, in addition to supporting the original livestock numbers, also supports about 200 elk. There is an excellent population of sage grouse as well as an excellent trout fishery. Another example is the Bunker S&G allotment which is in the center of the most overgrazed area in Central Nevada. The sheep on this allotment are grazed using a system of management that rotates light use over the allotment. The uplands are in good condition and the riparian areas are in good to excellent condition. While there was considerable soil lost from the stream channels on adjacent allotments during the floods of the early 1980's, the streams within the Bunker S&G remained essentially intact. According to Bill Platts of the Intermountain Research Station, the Central Nevada streams are extremely productive and have the potential of increasing fish production by three to five times. Several of the hardest hit streams provide habitat for the threatened Lahonton cutthroat trout.

The Toiyabe is finally tackling the problem of improving its range conditions. They are concentrating on the riparian areas because when they are managed correctly the remaining areas, for the most part, will also be managed correctly also. Most of the permittees that appealed the plan did so because the forest is implementing local plans to improve range conditions on their allotments. The appellants are Tony and Beulah Testolin, Jim Champie, LaVar Young, Wes and Mary Parsons, and Howard Wolf. From a range condition stand point these allotments are among the poorest on the forest. Utilization has been heavy for many years and very few of the desirable plants are left. The allotments involved are Bade Flat C&H and Tierney C&H. There have been several plans for these allotments all of which the permittees disregarded and did not follow. The permittees were very involved in the development of the current plans but felt that they could be disregarded as in the past. It was when they realized that the Toiyabe was serious about implementing the new plans that they appealed the Forest Plan.

All permittees are deeply involved in designing their allotment management plans. Once the plan is approved and implemented any significant adverse changes to the permittee are phased in over a period of years. For example, when stocking adjustments appear necessary they are handled as follows: Each year studies are made to determine when proper use is reached. The first year the permittee is encouraged to leave early once proper use is reached. The second year the permittee is asked to leave as soon as possible once proper use is reached. Then finally during the third year the cattle must leave so that proper use is not exceeded. The permits are not adjusted until after the third year. The Forest is doing everything possible to find alternatives for the permittees. On Bade Flat this last year the Forest cooperated with LaVar Young in developing additional water so that he could move to a new area and stay on the allotment longer. They offered Tony Testolin an additional month of grazing in an adjacent canyon and on an adjacent seeding. Tony refused the offer.

A strategy used by permittees for years has been to attack an administrator's personality when they are confronted by a resource issue. They have found it much more effective to focus on an individual officer. We often, in these situations, hear comments from permittees such as "We can't work with him", "We

weren't involved", or "He does't want to cooperate". This tact, in the past, has often resulted in a move for the administrator. His replacement normally will tackle other issues. This is exactly what is happening in Central Nevada. The permittees are complaining about individual forest officers and not focusing on the issue of poor range conditions.

Less than one third of the Toiyabe's livestock allotments are properly managed. During the next eight to ten years, five or six allotments per year will be placed under proper management. The resistance to changing the present management will be considerable, at least for the next three to five years.

TROUT UNLIMITED

PAMELA K. McCLELLAND
Resource Director

22 January 1988

Dr. Robert Behnke
Department of Fisheries & Wildlife Biology
Colorado State University
Fort Collins, Colorado 80523

Dear Bob:

Please find the information that has been circulated to our California and Nevada members concerning the Toiyabe Forest Plan. Thank you for your continued interest in Silver King Creek and the work with the Lahantan cutthroat trout. If you see any opportunities in this area that you can optimize please do so. If you see any areas in which we could be more effective in I would appreciate knowing.

Thank you. I look forward to hearing from you on Embrace-A-Stream.

Best wishes,

Pamela K. McClelland

Pamela K. McClelland

PKM/ch
Enclosures

Systematics and Evolution

III. Zoogeography of the Upper Kern Basin Trouts

by

Carl B. Schreck

Zoogeography of Fishes

Colorado State University

Dr. R. Behnke

Spring, 1968

Introduction

This is the third in a series of three papers discussing the systematics of the upper Kern basin trouts of California. The three currently recognized forms of Salmonids in consideration are the true golden trout, Salmo aguabonita, the Soda Creek golden trout, whitei, and the Kern River rainbow, gilberti. The latter two possibly have golden x rainbow ancestry. Morphological similarities with the inland cutthroat (pleuriticus?), and the Gila and Apache trouts of New Mexico and Arizona respectively, a chromosomal complement more readily derived from S. clarkii, and a karyotype identical to the Apache trout of Arizona suggests a lower Colorado basin origin of the ancestral golden trout. The intent of this discussion is to determine the most likely zoogeographic route followed by the progenital aguabonita stock from the ~~Great Basin~~ lower Colo to the upper Kern system.

Previous Hypotheses

Rounsefell (1962) suggested that the ancestral home of the salmonids was probably in freshwater. According to Mottley (1934), the progenitor of North American Salmo became separated from other fishes of this family during the next to the last glacial period and became localized on the eastern side of the continent. Then, during the interglacial period, the trout was able to migrate across to the Pacific coast. Mottley goes on to say that the cutthroat trout evidently was isolated earlier than the rainbow because it is now "more clearly distinguished." The present forms of clarkii and gairdneri were segregated from the general circumpolar "distribution by the last glaciation and either they were forced southward along the Pacific drainage basin, or only the more southern populations survived.... After the ice melted the rainbows and cut-throats moved northward penetrating the old territory and recolonizing it as conditions become suitable...." As the land rose, populations of rainbows became isolated and new varieties were formed. Mottley's conclusions are speculative and are not based upon ichthyological evidence, a fact also true of most other hypotheses about the distribution of Salmo.

Jordan expressed varying and often contradictory views about how the trout came to California and the Kern basin. He felt that S. clarkii entered the United States by moving southward down western North America to the Columbia River (Jordan, 1894, 1899, 1906), and the rainbow speciated from it in the Cascade Range. The cutthroat trout crossed the Continental Divide, and thus established itself in the Missouri system; during the glacial epoch the whole Utah basin was part of the drainage of the Columbia. From east of the divide, it crossed back again from the Rio Grande to the Colorado basin. Jordan (1894) expressed the view that in the glacial period the melting ice formed lakes through which the primitive

How various authors explain Kern trout.

I: rainbow from coast - isolated
- speciate

Ia: rainbow - Shasta or Cascades

II: cutthroat or "unknown" progenitor from Colo. R.

III - Combination of hybrids of I & II

a. Point where cutthroat became rainbow.

b. golden still cutt. (mykiss)

cutthroat trout came over the Sierras into California. The Kern and San Joaquin were the first drainages settled by these migrants. Those in the San Joaquin gave rise to the coastal cutthroat whereas those in the Kern speciated into the rainbow trout. Thus, according to this view, the Kern basin was the birthplace of S. gairdneri. In 1899, however, Jordan (1899) stated that "while it is possible that the Kern trout (gilberti) came from the Colorado trout (pleuriticus), which is greatly resembles,.... they [probably] did not" because the main crest of the Sierra Nevada would be too formidable a barrier. Instead, an isolated cutthroat population in the Cascade Range gave rise to the steelhead trout which became the parental form of both the Shasta and the Kern trouts.

Evermann and Bryant (1919) are in agreement with Jordan's earlier views. They felt that the glacial melt formed the waterways followed by the trout of the Colorado system to migrate into certain headwater tributaries of the San Joaquin drainage. The Kern was settled early by these fish, and they would go out from the Kern into Tulane Lake which was "then much larger and much colder than it has ever been since." Hubbs (1946) states that gairderni was no doubt native to southern California.

In Jordan's 1892 description of aguabonita he stated that the golden trout is an off-shoot or descendant of the cutthroat trout and that its nearest relative is the form called pleuriticus. He further said that aguabonita is in no way related to S. gairdneri. Ferguson (1916) also expressed the belief that the presence of the golden trout in the Kern basin antedates the invasion of the coastal rainbow. Jordan (1928), however, revised his last published opinion completely and stated that aguabonita and whitei were actually derived from isolated populations of the Shasta trout, S. shasta, and not from isolated populations of the Kern River rainbow. Snyder (1933) reported that the Kern goldens may simply be a

color varient of the Shasta trout. All the other literature, including Jordan's, on this subject suggests that gilberti speciated from an isolated coastal rainbow. Remote populations of the Kern River trout then became secure from upstream invasion by the formation of impassable waterfalls and gave rise to aguabonita, in Golden Trout Creek and the South Fork of the Kern, and to whitei in the Little Kern drainage (Schreck, 1967. Trouts of the upper Kern Basin, California. Mimeo. obtainable from the Colo. Coop. Fish. Unit., Colo. State Univ., Ft. Collins, Colo.).

Faunal Evidence

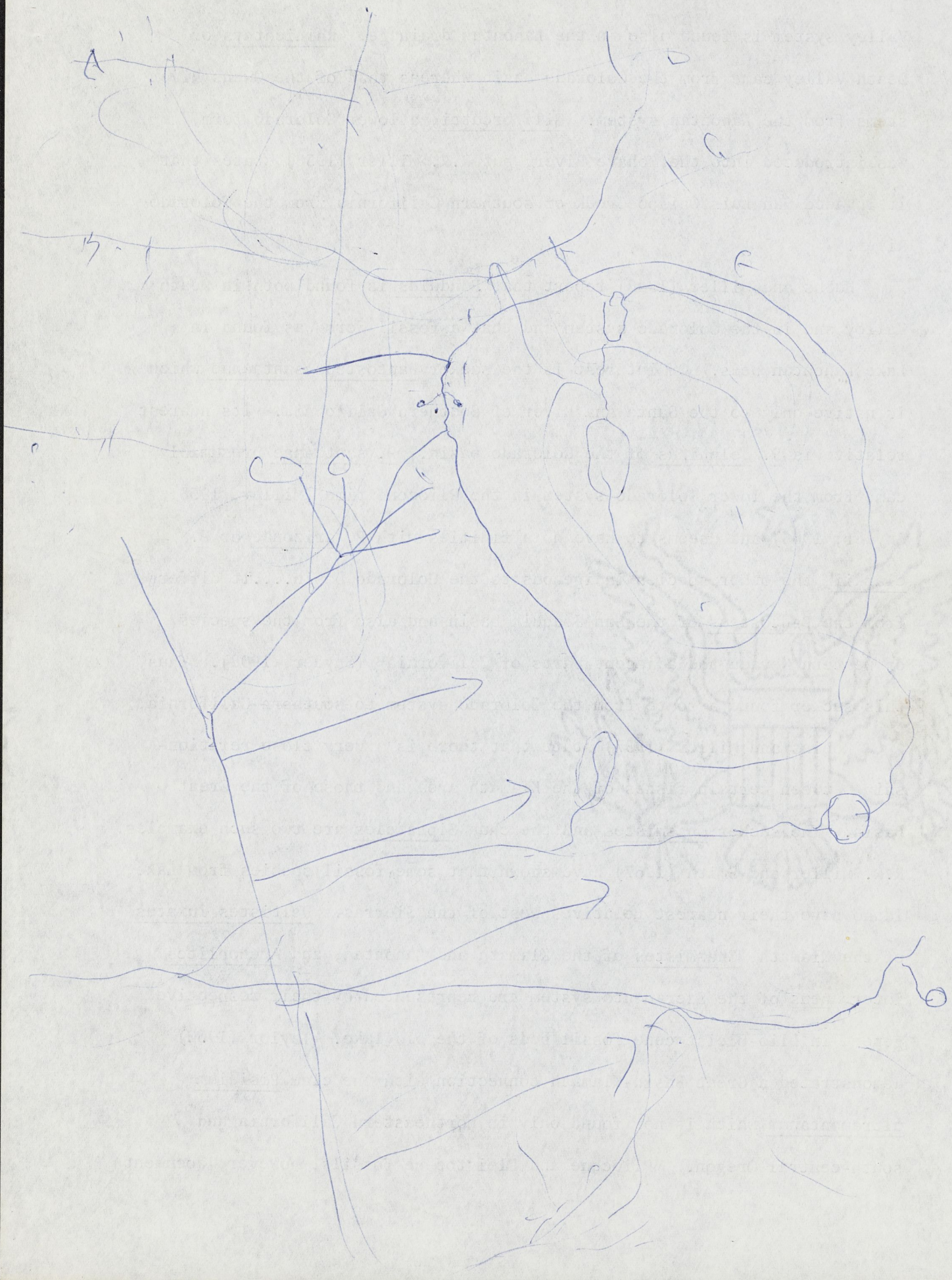
R.R. Miller (1946) cites physiographic evidence showing that during the late Pleistocene an integrated river and lake system was in several desert basins in eastern California and southwestern Nevada; Death Valley apparently was the sump. Fossil and living fish distribution in concert with physiographic data demonstrate possible connections between this Death Valley System and the Lahontan basin to the north as well as with the lower Colorado River drainage to the south and east. That the nascent golden came into California via the former route is improbable because no relict populations have been found in this area although suitable habitat is available.

R.R. Miller (1946) states that a Cyprinodon of the Owens Valley, Death Valley, and middle and lower Amargosa River basin originated from the lower Colorado system, the only other place where this genus is found. Fossils of this species have also been found in Tertiary or early Quaternary beds in Death Valley; this demonstrates that the Colorado-Death Valley connection was ancient. Living and fossil (Pleistocene) Siphateles are found in both the Owens-Mohave system and in the Lahontan basin as is the cyprinodont Eurpetrichthys. An ancestral Catostomus of the Death

Valley system is found also in the Lahontan drainage. Rhinichthys of Death Valley came from the Colorado basin whereas that of the Owens River stems from the Lahontan system. Gila orcutti, a lower Colorado form, was introduced into the Mohave River, but R.R. Miller (1958) states that it invaded San Luis Obispo Creek of southern California from the Colorado River.

Hubbs and Miller (1948) report that Fundulus is found both in Death Valley and in the Colorado system and that a fossil form was found in Lake Lahontan beds. Of interest is the sucker Pantosteus santaanae which is native only to the Santa Ana River of Southern California. Its nearest relative is P. delphinus of the Colorado basin. P. santaanae presumably came from the lower Colorado system in the Pliocene time (Miller, 1958; Snyder, 1908) and "seems to have no affinities with P. arizonae or P. clarkii, the other species indigenous to the Colorado basin....It differs from the Pantosteus of the San Joaquin basin and also from the species of western Nevada and adjacent parts of California" (Snyder, 1908). Thus, this sucker found a route from the Colorado system to southern California.

Robins and Miller (1957) state that there is a very close relationship between certain fishes of the Klamath area and those of the Great Basin. The sucker Chasmistes and the chub Siphateles are two such examples. R.R. Miller and Smith (1967) have shown that some fossil species from Lake Idaho have their nearest relatives west of the Sierras. Deltistes luxatus of the Klamath, Chasmistes of the Klamath and Lahontan, and Archoplites interruptus of the Sacramento system are represented by their respective genera in Plio-pleistocene fossil beds of the old lake. Taylor (1960) demonstrated a Great Basin-Klamath connection with the clam Pisidium ultramontanum which is now found only in northeastern California and south-central Oregon. "Pliocene and Pleistocene fossils, however, document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its former occurrence in the Snake River drainage as far east as southeastern Idaho." Other mollusks such as the snail Ceriphasia also shows this. "These links form a chain which leads from Walker Lake in western Nevada across Eagle Lake and the upper Pit River, California, to Klamath Lake, Oregon; thence across Fossil Lake and the Malheur basin, Oregon, to the Snake River; and through Gentile Valley and Bear Lake, Idaho, to Utah Lake, Utah....These lakes are therefore thought to have been connected, although not necessarily all at once." This Great Basin - Klamath connection has been discussed to illustrate how aquatic fauna could surmount the obstacle of a mountain range. Also, there is a golden-like salmonid present in the upper Pit and McCloud River drainages, California, which at one time may have had a more broad distribution.

R.R. Miller (1950) feels that S. clarkii pleuriticus, "like other representatives of S. clarkii which entered the Platte, Arkansas, and Rio Grande basins, gained access to the Colorado via headwater connections." S. gilae, once native to tributaries of the Salt and Gila rivers of New Mexico and Arizona and to the headwaters of the Little Colorado River, however, employed a different route. Miller states that the Gila trout may have entered this area during the Pleistocene via the Gulf of California. At that time, there was a major submergence of Baja California and the ocean and air temperatures may have been considerably lowered by glacial runoff. This would have allowed the progenitor of the Gila trout to cross over or go around the peninsula of Baja from the Pacific Coast to Arizona and New Mexico. It is, of course, possible that the golden Stammform originated from this ancestral Gila, but, because of their similarities to the Colorado cutthroat, a polyphyletic origin from S. clarkii is probably more in accord with what actually transpired. The Apache trout of Arizona most certainly had a similar origin.

Although a zoogeographic route for a lower Colorado trout to follow from the lower Colorado system to the Owens Valley has been demonstrated, no pathway over the main crest of the Sierras has yet been shown (Miller, R.R., 1946). A.H. Miller (1951) with reference to birds, however, states that the fauna of both the Kern and the Shasta areas show great affinities with that of the Great Basin, and may serve as a "bridge" over the Sierras. There is no real barrier to the Kern from the east; this area is experiencing rapidly shifting climatic and vegetational conditions. "Since the elevation of the Sierra Nevada in the Pliocene, the Great Basin [avian] fauna has been fairly sharply excluded from western and central California... At present we are probably in a stage of reopening connecting avenues as in the Shasta and upper Kern valley's" (Miller, A.H., 1951).

Geographical Considerations

A study of annectent watersheds that would allow the coastal rainbow to invade the lower Kern is appropriate here. Even though the presence of aguabonita in the headwaters of the Kern probably antedates that of gairdneri, the latter still plays a major role in the formation of the present fish fauna of this area.

In relatively recent times the whole lower part of California's Central Valley was occupied by an immense lake, Lake Tulare, which during periods of overflow connected the Kings, Kaweah, and Kern rivers (Hubbs and Miller, 1948). Lake Tulare has been dated back to the middle or late Wisconsin (Miller, R.R., 1965), and prior to 1878 it would overflow into the San Joaquin system when the Kings River would flood (Davis, Green, Olmstead, and Brown, 1959).

There is other evidence suggestive of the fact that Sierran west slope rivers may have had a historic connection. According to a collection

of papers edited by Wright and Frey (1965), the Pacific Ocean was much lower during stages of glaciation; one study says by as much as 350 to 400 feet, and another feels that the sea actually was 1,200 feet lower than at present. Thus, during periods when the ocean had receded, the historic rivers could have had confluence out in the area now covered by salt water. This would have allowed the primary, or other fishes restricted mainly to fresh water, to move from one drainage basin to another. Hershey (1902) states that is was in the Pleistocene that the sea retreated to its present level after a final invasion; also, in the Quaternary, there was a general uplift of southern California. S. gairdneri, considered a secondary freshwater fish, could have entered drainage basins by migrating through the sea from the mouth of one river to that of the next.

Kern Geomorphogeny

On May 7, 1776, Father Francesco Graces named a southern Sierra Nevada river Rio de San Felipe; the Indians had called it Po-sun-co-la. In 1846 John C. Fremont renamed this stream in honor of the artist Lieutenant Edward Mayer Kern.

The Kern River has a 155 mile course and has an annual runoff of about 700,000 acre feet. Eighty percent of this water originates from tributaries along the first 15 miles of the stream; the upper portion of the Kern is in Sequoia National Park and drains approximately 400 square miles. The Kern canyon is unique among Sierran valley in that it is the only one with a north-south direction (Pacific Gas and Electric Company, 1962).

According to Lawson (1904), the Kern canyon was formed by a "Graben;" the crack in the earth was then modified by the action of erosion and glaciation. Matthes (1937) states that the Kern's direction was determined by a fault, "a long fracture in the Sierra block, but to judge from the

older features of its landscape and from its great breadth, the upper Kern basin as a whole has been developed from a very ancient valley.... It probably antedates the fault, though it is possible that the fault, too, is of great antiquity."

Lawson (1904) felt that the upper Kern area had three possible historic drainage patterns; the most probable is as follows. The valley through which Golden Trout Creek and the South Fork of the Kern now flow (Toowa Valley) is the lowest point in the rim of the upper Kern drainage, excepting the present outlet. "The Chagoopa Plateau....is the ancient floor of the [Kern] basin before it was trenched by the canon of the Kern." The Little Kern plateau and Toowa Valley were apparently historically interconnected with the Chagoopa surface prior to their uplift. At this time the whole upper Kern watershed drained out of this area through Toowa Valley eastward to a gap in the summit crest "and thence out into the region of the Great Basin at the south end of Owens Lake, or it turned, following the course of the South Fork, and joined with the high valley represented by Little Kern Plateau lower down on the Kern." The latter may actually be the case, but there is no real evidence in support of it. If the former hypothesis were true, then the Kern abandoned the Toowa Valley route after the main uplift of the Sierras. Lawson stated that there were two distinct uplifts, the first of which inaugurated the westward tilting of the peneplane. This took place approximately at the start of the Quaternary.

Webb (1946), contrarily, reports that the study of erosional levels, reconstructions of dissected drainage divides, and geological relations of a volcanic series proves that the Kern River has always flowed in a southerly course. Thus, Toowa Valley drained westward at the time that the Kern was graded to the Chagoopa surface, and, consequently, it must

have had a westward slope during the "Chagoopa cycle." Webb goes on to say that the present-day Kern Canyon was formed by a fault as the "structural control agent " and not by Lawson's Graben. The fault had its final displacement prior to the development of the Chagoopa surface. "An even more ancient date is suggested because the fault (and river) cut diagonally across the Great Western Divide; this may mean the fault is pre-Divide in development....The Kern might not have shifted from its southerly course during the westward tilt given by the Sierra Nevada fault, since the master drainage was established in pre-Chagoopa time when the region had considerable relief" (Webb, 1946). In any case, the flow of the Kern was established early in the uplift of the Sierras.

If the only barrier between the Kern drainage and the Owens Valley (and the lower Colorado system) is the Main Crest of the Sierras, an understanding of the formation of this wall could show a zoogeographic route over it. Matthes (1937) proposes the following geomorphogeny of the southern Sierra Nevada and the Main Crest. In the Mesozoic, about 100,000,000 years ago in the area now occupied by the Sierras, there arose a system of mountains. The present location of these mountains was historically sometimes occupied by the ocean. These "ancestral Sierras" existed for many millions of years until they were worn down by erosion. All that then remained was a low row of hills in a peneplane sloping gently towards the sea. At this time, the streams flowed mainly northeasterly or southeasterly between the hills. After the onset of the Cenozoic, about 50 to 60 million years ago, the first uplift of the modern Sierras took place. The whole block of hills tilted to the southwest, and as a result the main streams altered their course to flow in this direction; many lesser rivers, however, maintained their original direction of flow. The Kern canyon stems possibly from a very ancient valley present in these historic Sierras and was about

500 feet above sea level in elevation. This valley antedates the fault which is responsible for determining the straight course of the Kern.

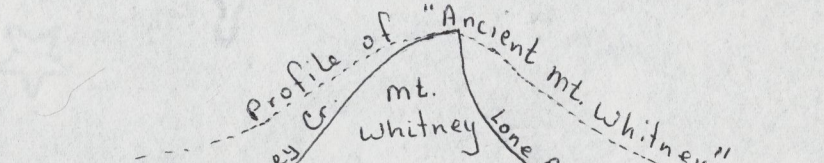
The initial uplift and tilting caused the streams to intrench themselves a thousand feet or more on both sides of the Main Crest. Erosion wore the mountains round again. The second uplift caused a repetition of these processes; the Chagoopa surface is clearly a "remnant of the former floor of the Kern Basin that was developed to a great breath during an erosion cycle following a third uplift...." (Matthes, 1937). The Kern canyon was trenched in consequences of the last great uplift which took place at about the beginning of the Ice Age. At this time, the Main Crest of the Sierras was also raised to its present altitude.

Several miles east of the incipient mountain range was another longitudinal valley of great antiquity. This valley did not raise with the Sierras, and it was the down-faulting of this depression after the Sierras had attained approximately their present height and had undergone their first glaciation that created the imposing eastern front of the Sierras. Thus, the precipitous face of the Main Crest was created during the first half of the Ice Age through the periodic sinking of the land to the east. This valley was to become that of the Owens. The eastern front of the Sierra range became molded twice more by glacial action (Matthes, 1937).

The Kern Canyon of today is approximately one million years old, and the Chagoopa cycle dates back about ten to fifteen million years. The Boreal Plateau cycle may have required twenty million and possibly another ten million years elapsed between this cycle and the initial uplift of the Sierras. Thus it has taken 35-45 million years to evolve the present day Sierra Nevada from the low hills remnant of the ancient mountains. Wright and Frey (1965) state that the Sequoia area had its uplift in the late Pliocene or early Pleistocene and that the Kern Canyon was

almost all cut by Pleistocene times. Bateman and Wahrhaftic (1966) date the Kern Canyon by showing that the cutting of the Little Kern River into basalt flows by its mouth was in material 3.5± 0.1 million years old. The bulk of the gauging of the upper Kern Canyon was completed by that time, and thus the Kern fault has been inactive for at least that many years, probably much longer.

The ancestral golden trout, finding entry into the Owens Valley from the Death Valley system and the annectent lakes from the lower Colorado basin during some early period of glacial runoff, reached the eastern base of the Sierras. From here, it crossed over the Main Crest of the Sierra Nevada. As Evermann (1906) points out, "occasionally by eating back into the watershed one stream may steal a portion of the headwaters of another on the other side of the divide, and fishes sometimes enter a water course in that way." Thus through the evolution of the eastern wall of the Sierras and through stream capture, the ancestral aguabonita may have entered the Kern drainage. Matthes (1937) illustrates the change in geomorphology of Mount Whitney and its related streams as follows:



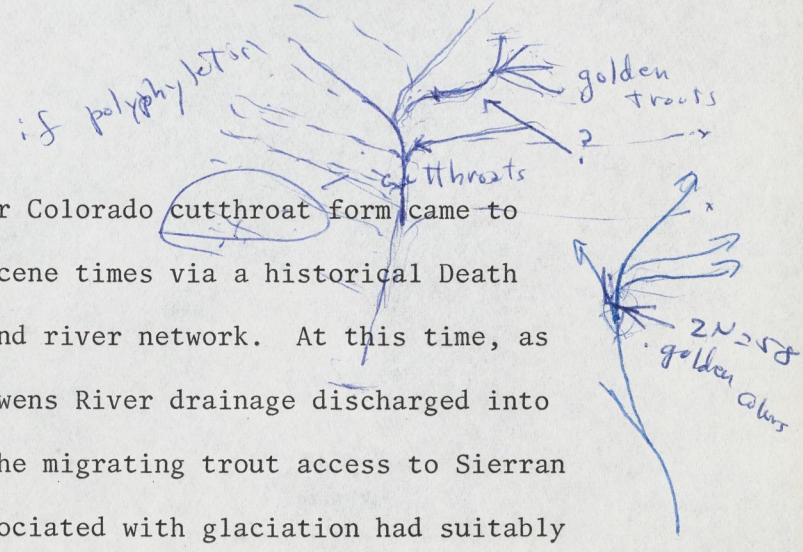
This diagram is presented merely as an example of stream capture and does not mean to suggest that this was the actual route followed by the migrating trout.

The diverging Salmo now in the Kern area, and possibly much further north also, became the incipient golden trout. S. clarkii is more well suited to a boreal existence than the rainbow; this is shown by the cutthroat's predelections and distributions (Miller, R.R., 1950). Lawson (1904), Matthes (1965), and Webb (1946) state that the headwaters of the South Fork of the Kern historically flowed down Golden Trout Creek. Volcanic activity, followed by erosion, caused the South Fork to assume its present course. Presently, the two streams are separated by a mere few hundred yards. In the late 1800's, there was also a connection (tunnel) made between Golden Trout Creek and the South Fork of the Kern through the narrow strip of land that now isolates them; this undoubtedly allowed the passage of aguabonita to pass from the former into the latter (Evermann, 1906). In any case, the origin of the lower portion of the South Fork of the Kern is still obscure (Webb, 1946), and it is of interest to determine whether or not this lower section could have served as the connection to the east.

If the trout came over the Main Crest as has been proposed, the following question must next be answered. Why is the distribution of Kern trouts so limited? As Evermann (1906) has pointed out, all of the tributaries to the Kern north of Golden Trout Creek were barren of fish when the White man first came to this area. Why also, were the streams of the eastern face of the Sierras barren of fish in this region if the migrating trout used them as a means to enter the Kern?

Lawson (1904) and Matthes (1965) discuss the glaciation of the upper Kern area. Their conclusions are more or less in agreement, and Matthes explains this process as follows: There were two distinct stages of glaciation - "a later one, the Wisconsin, and an earlier one, El Portal, separated by a lengthy time interval; meager indications were also found

of a third, a very early stage, the Glacier Point." These three periods of extensive and long-continued glaciation took place in the Pleistocene Epoch; the Wisconsin was in the late Pleistocene. The extent of the glaciation declined with each successive stage. Little is known about the Glacier Point glaciation. The El Portal stage of the Kern Canyon, however, is known to have its southern limits extend about eight miles south of the mouth of Golden Trout Creek to the vicinity of Hockett Peak. The southern extent of the Wisconsin glacier in the valley is down to about one mile south of the Kern-Golden Trout Creek confluence. These two stages of glaciation completely covered the Kern River and all of the tributaries to the main Kern north of Golden Trout Creek on the east and north of the Little Kern on the west. The trunk glacier extended for only a mile or so up Golden Trout Creek. Thus, except for the extreme headwaters of the Little Kern River and Golden Trout Creek, the localities of whitei and aguabonita found by White Man were left unglaciated. All fishes north of these two streams were decimated by the glaciation (see map). Matthes (1937) also states that the streams east of the Main Crest were covered with ice, thus any trout there would also have disappeared.



Summary of Zoogeographic Events

In summary, the primitive lower Colorado cutthroat form came to southern California in Plio-Pleistocene times via a historical Death Valley-Lower Colorado system lake and river network. At this time, as Hubbs and Miller (1948) show, the Owens River drainage discharged into the Death Valley Sump. This gave the migrating trout access to Sierran east slope streams. Conditions associated with glaciation had suitably cooled the annectent lakes to facilitate this passage. The geomorphogeny

of the Kern area reveals that geomorphic evolution of the Sierras combined with stream capture could have given the incipient goldens entry into the Kern basin or into some interconnecting area west of the Main Crest. The nascent fish could now distribute themselves (primarily in boreal habitats because of predetermined predelections) throughout much of the southern Sierras; there is, however, no evidence suggestive of the latter occurrence. Subsequently, in the Pleistocene, most of the Sierran drainages became glaciated, and their fish faunas were destroyed. The only portion of the upper Kern basin (southern Sierra Nevada) not glaciated was the Golden Trout Creek-South Fork of the Kern complex and the Little Kern drainage. It is interesting to note here that the only other area of the Sierras not covered by ice was that of the upper McCloud and Pit basins which also contain a unique, possibly golden-like trout (Personal communication from Dr. D. Seegrist). Stebbins (1954) reports that salamanders of the genus Hydromantes have a similar disjunct distribution. H. platycephalus has a range from Sequoia National Park north to Sonora Pass, whereas H. shastae is found only in Shasta County.

The relict populations in Golden Trout Creek and the South Fork of the Kern were able to speciate into aguabonita. As the glaciers retreated, the coastal rainbow was able to invade the upper Kern; its presence in the lower portion of the system was due to conditions previously discussed. Waterfalls that had formed on Golden Trout Creek isolated the trout above it, but possibly prior to the rainbow, golden trout were free to pass down into the Kern River. In the Kern, aguabonita hybridized with gairdneri and through introgressive hybridization formed gilberti. A similar process occurred in the Little Kern drainage, and crosses between the indigenous trouts and gairdneri formed the salmonid now known as whitei.

Evermann and Bryant (1919) state that barriers formed on the lower ends of the South Fork of the Kern and the Little Kern River, but this conclusion is apparently unwarranted and not based on any evidence. Barriers similar to these on Golden Trout Creek, however, did form on the other tributaries to the upper Kern River, and thus they were secured from reinvasion of the Kern trouts. - To explain why streams were barren? or for maintaining purity?

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A KEY, BASED ON SCALES, TO THE FAMILIES OF NATIVE CALIFORNIA FRESHWATER FISHES

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ABSTRACT: Much interdisciplinary interest has been shown with regard to fish scales in addition to their use in fisheries biology. To aid future workers, a key to the scales of the native California freshwater fish families is presented along with photomicrographs of scales from each group.

INTRODUCTION

Fish scales have been used in fisheries biology and systematic ichthyology for many years. Within fisheries studies, emphasis has been placed upon the use of scales in age and growth studies (Cable, 1956; Cating, 1954; Chugunova, 1959; Cooper, 1951, 1952; Fry, 1943; Hile, 1936; Hogman, 1970; Jensen and Wise, 1961; Miller, 1955; Phillips, 1948; Rush, 1952; Schuck, 1949; Taylor, 1916; Whitney and Carlander, 1956; Meehean, 1935). Various keys, based upon the morphology of scales, have been published dealing with species identification within families and with the identification of families comprising regional fish faunas (Batts, 1964; Lagler, 1947; Koo, 1962).

Fish scales have been used in palaeontological work (David, 1944, 1946a, 1946b), sediment analysis (Lagler and Vallentyne, 1956; Pennington and Frost, 1961; Soutar and Isaacs, 1969), and archaeology (Follett, 1967a, 1967b; Hubbs and Miller, 1948). Even within fisheries work, scales have been encountered during analysis of the stomach contents of various fishes (Greenfield, Ross, and Deckert, 1970; Kimsey, 1954). Based upon this evidently wide interdisciplinary interest in and use of fish scales, it is felt that a scale-based key to the families of native freshwater fishes of California would be a useful aid.

TABLE 1. *Species examined.*

Species	Source
Thaleichthys pacificus	CAS[1]
Oncorhynchus tshawytscha	UCD[2]
O. kisutch	CAS, UCD
Salmo gairdnerii	UCD
S. g. gairdnerii	UCD
S. g. stonei	UCD
S. g. gilberti	CAS
S. g. aquilarum	CAS
S. clarkii clarkii	CAS
S. c. henshawi	CAS
S. c. seleniris	CAS
S. aguabonita aguabonita	CAS
S. a. whitei	CAS
Salvelinus malma parkei	CAS
Prosopium williamsoni	CAS
Xyrauchen texanus	CAS
Catostomus luxatus	CAS
C. platyrhynchus	CAS
C. santaanae	CAS
C. rimiculus	CAS
C. latipinnis	CAS
C. occidentalis occidentalis	UCD
C. o. humboldtianus	CAS
C. mniotiltus	CAS
C. tahoensis	CAS
Rhinichthys osculus klamathensis	CAS
Mylopharodon conocephalus	CAS, UCD
Orthodon microlepidotus	UCD
Pogonichthys macrolepidotus	UCD
Lavinia exilicauda exilicauda	UCD
L. e. harengus	CAS
Ptychocheilus grandis	UCD
Hesperoleucas symmetricus symmetricus	UCD
H. s. subditus	CAS
H. s. venustus	CAS, UCD
H. navarroensis	CAS
H. parvipinnis	CAS
Gila bicolor bicolor	CAS
G. b. obesa	CAS, UCD
G. b. pectinifera	CAS
G. mohavensis	CAS
G. crassicauda	CAS
G. orcutti	CAS

[1] CAS = specimens from California Academy of Sciences, San Francisco.
[2] UCD = specimens from the author's personal collection, presently at University of California, Davis.

TABLE 1. (*continued*)

Species	Source
G. elegans	CAS
Richardsonius balteatus egregius	CAS
Cyprinodon macularius californiensis	CAS
C. nevadensis nevadensis	CAS
C. n. calidae	CAS
C. n. shoshone	CAS
C. salinus	CAS
Fundulus parvipinnis	CAS
Mugil cephalis	CAS
Archoplites interruptus	UCD
Hysterocarpus traskii	CAS, UCD

For the purposes of this paper, native freshwater fishes will refer to those fishes which occur exclusively in freshwater or spend a significant portion of their life-cycle in freshwater and which occurred in California prior to the known introduction of exotic species during and after the nineteenth century (Kimsey and Fisk, 1960; Shapovalov, Dill, and Cordone, 1959; Walford, 1931). The only exception has been the inclusion of the Mugilidae because of their importance in the Colorado River.

METHODS AND MATERIALS

The scales studied come from 54 species of native fishes (table 1) and represent specimens collected by the author or by members of the California Department of Fish and Game, and specimens from the California Academy of

TABLE 2. *Scale sampling locations.*

A. Row anterior to dorsal fin.
B. Right side, below dorsal fin, above lateral line.
C. Left side, below dorsal fin, above lateral line.
D. Right side, below dorsal fin, below lateral line.
E. Left side, below dorsal fin, below lateral line.
F. Right side, caudal penduncle, above lateral line.
G. Left side, caudal penduncle, above lateral line.
H. Right side, caudal penduncle, below lateral line.
I. Left side, caudal penduncle, below lateral line.
J. Row posterior to dorsal fin.

TABLE 3. *Scale characteristics of California freshwater fish families.*

Family	Ctenoid Scales	Cycloid Scales	Scutes	Neither
Petromyzonidae				X
Acipenseridae			X	
Osmeridae		X		
Salmonidae		X		
Catostomidae		X		
Cyprinidae		X		
Gasterosteidae			X	
Cyprinodontidae	X	X[3]		
Mugilidae	X			
Centrarchidae	X			
Embiotocidae		X[3]		
Cottidae				X

[3] Scales of these families, while being cycloid, should be oriented as shown for ctenoid scales in figure 1 b.

Sciences, San Francisco. Table III indicates the general scale characteristics of the fishes in this study.

The fish were sampled for scales from ten different body locations (table 2) on the author's specimens. For reasons of future use, the specimens from the California Acadamy of Sciences could only be sampled from six locations on the right-hand side of the fish. Wherever possible, samples were taken from several individuals of different sizes within a species in order to allow for ontogenetic variations. All scale samples were mounted in glycerine jelly on microscope slides (Weesner, 1960) and examined under a dissecting microscope at between ten and thirty magnifications.

DEFINITIONS

The terms used here to describe the surface features of scales are taken from Lagler (1947, pp. 150–151) and are illustrated in figure 1.

Circuli — "Elevated markings on the outer surface; usually appearing as lines which more or less follow the outline shape of the scale."

Focus — "First part of scale to appear in growth; often central."

Radii — "Grooves, usually more or less radiating from focus to one or more margins."

Primary Radii — "Radii that extend from focus to margin."

Secondary Radii — "Radii that begin outward from, not at, focus."

Ctenii — "Tooth-like structures on posterior portion of scale."

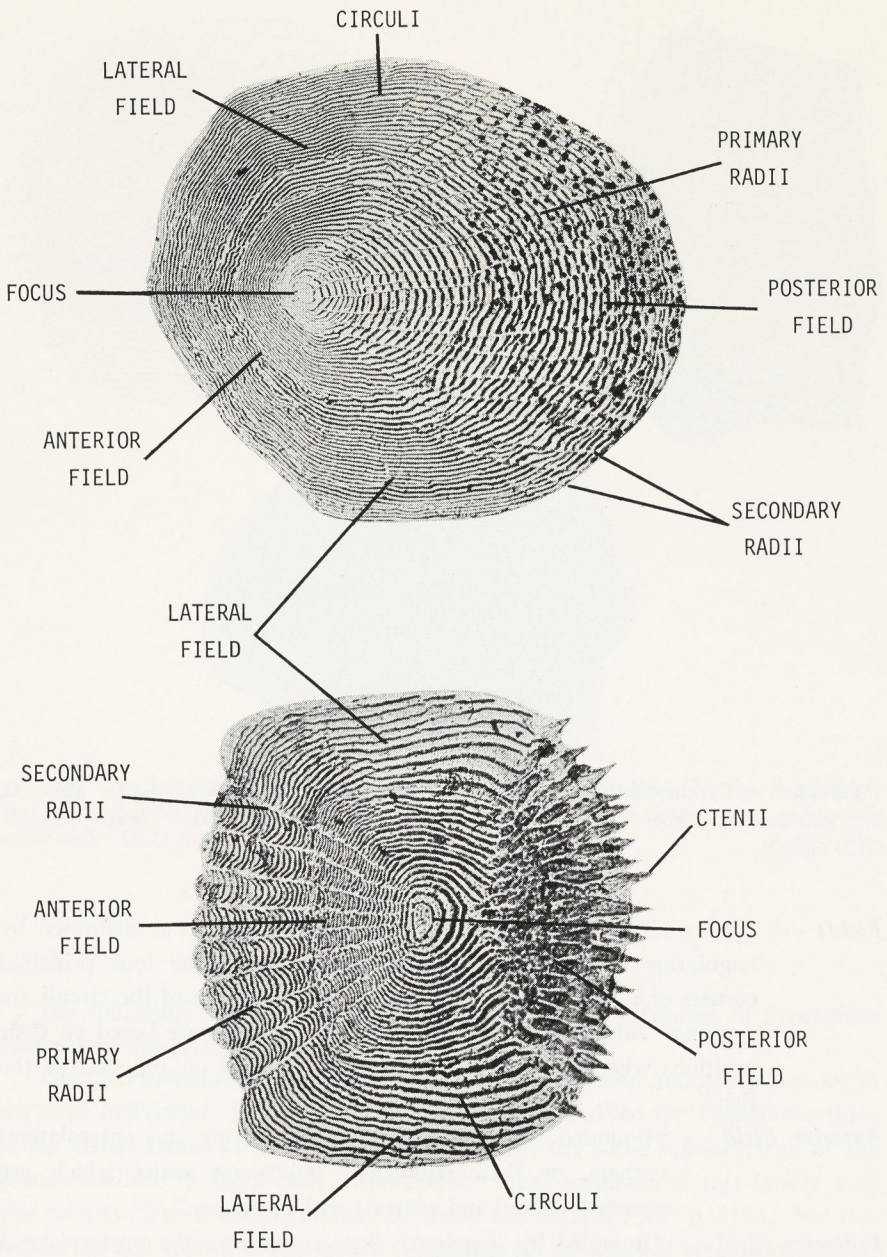

FIGURE 1. Top. Cycloid Scale. *Cyprinidae. Mylopharodon conocephalus.* UCD 5040 C. Bottom. Ctenoid Scale. Centrarchidae. *Archoplites interruptus.* UCD 5021 E.

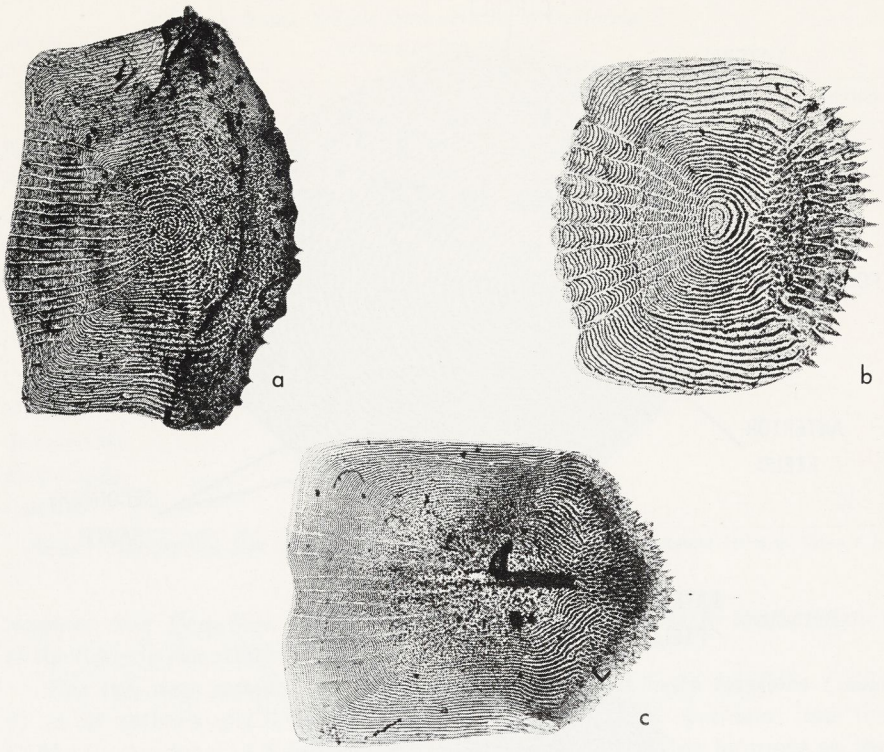

FIGURE 2. a. Cyprinodontidae. *Cyprinodon macularius californiensis*. UCD 5063 G. b. Centrarchidae. *Archoplites interruptus*. UCD 5021 E. c. Mugilidae. *Mugil cephalus*. UCD 5056 I.

Fields — "Areas of the outer surface of the scale, either real as delimited by angulation of the ridges (circuli) at levels of the four principal corners or imaginary if the corners or configuration of the circuli are wanting. Adjectives of direction applied to fields are based on their positions when the scales are normally situated on the side of the fish."

Anterior Field — "Bounded by imaginary lines connecting the anterolateral corners, or their equivalent points on scales which are rounded (dorsal and ventral) with the focus."

Posterior Field — "Bounded by imaginary lines connecting the posterolateral corners (dorsal and ventral) with the focus."

Lateral Fields — "Dorsal and ventral fields remaining after delimitation of anterior and posterior ones."

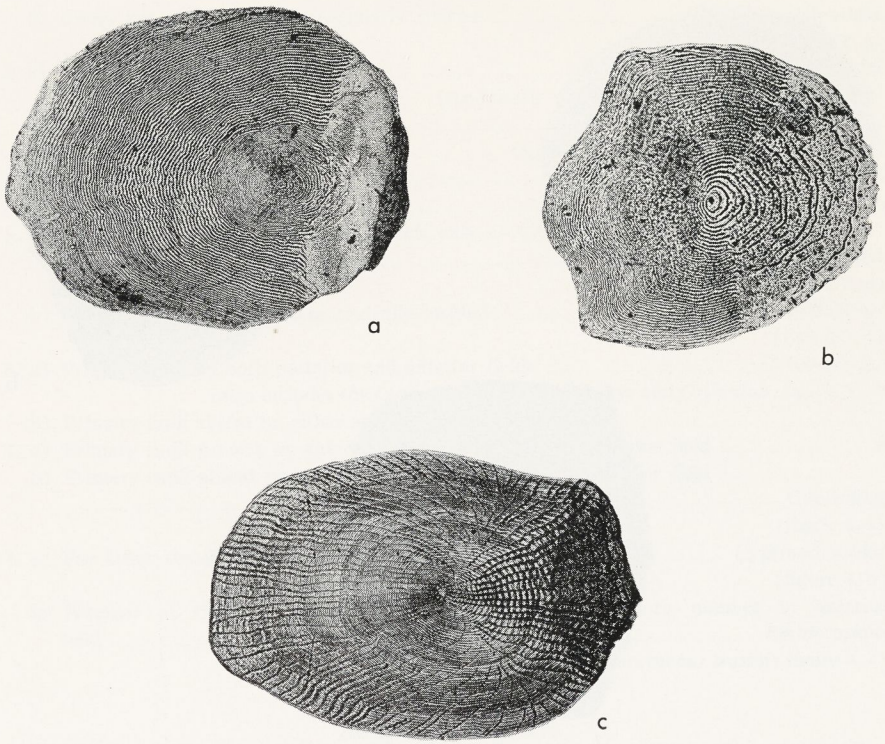

FIGURE 3. a. Salmonidae. *Salmo gairdnerii gairdnerii*. UCD 5002 D. b. Salmonidae. *Prosopium williamsoni*. UCD 5016 C. c. Catostomidae. *Catostomus occidentalis occidentalis*. UCD 5026 C.

SCALE-BASED KEY TO THE FAMILIES OF CALIFORNIA FRESHWATER FISHES

The following is a key to the family level with the exception of *Prosopium williamsoni* which is identified to species.

The Cyprinodontidae are characterized by both ctenoid and cycloid scales in the same individual. Lagler (1947, pp. 156–157) classified the Cyprinodontidae of the Great Lakes as having cycloid scales and the same appears true of the genus *Fundulus* in California. However, the other members of this family may also possess ctenoid scales (Lagler, Bardach, and Miller, 1962, p. 114). For this reason the key identifies this family twice, once on the basis of ctenoid scales and again on the basis of cycloid scales. This same case appears true of the Centrarchidae (Lagler, Bardach, and Miller, 1962, p. 114). Based upon data from my collections, however, I find cycloid scales to occur only once in 32 samples and

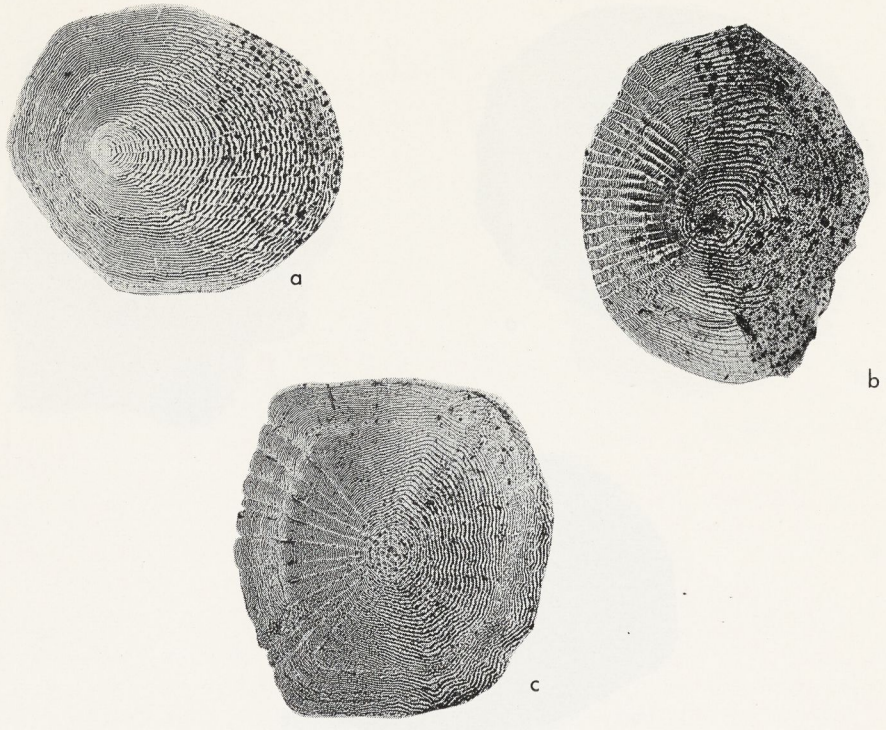

FIGURE 4. a. Cyprinidae. *Mylopharodon conocephalus*. UCD 5040 C. b. Cyprinodontidae. *Cyprinodon macularius californiensis*. UCD 5063 A. c. Embiotocidae. *Hysterocarpus traskii*. UCD 5099 C.

then only from restricted areas of the body in centrarchids (table 2, A). This is a rather low frequency and if one considers the total number of scales over a fish's body, it appears that occurrence of cycloid scales in *Archoplites interruptus* will be even more rare. I agree, therefore, that "These fishes may still be considered as predominantly ctenoid in their squamation but the degree and extent of development of the ctenii varies from place to place on the body" (Lagler, Bardach, and Miller, 1962, p. 114). In the rare event that a cycloid scale from this family should present itself in isolation it will key out as representing the Embiotocidae instead of the Centrarchidae.

Figures 2, 3, and 4 illustrate each of the families or species separated by the key. Each illustration is oriented with the anterior field to the observer's left.

1. a) Ctenii present on posterior field 2
   b) Ctenii absent on posterior field 4
2. a) Ctenii numerous and evenly spaced 3

b) Ctenii not numerous and irregularly spaced ..... Cyprinodontidae
(figure 2, a)

3. a) Radii converge toward focus ..... Centrarchidae
(specifically *Archoplites interruptus*; figure 2, b)

b) Radii roughly parallel ..... Mugilidae
(specifically *Mugil cephalus*; figure 2, c)

4. a) Scale cycloid without radii 5

b) Scale cycloid with radii 6

5. a) Scale with anterior and posterior fields only or without fields .....
..... Osmeridae and Salmonidae
(figure 3, a)

b) Scale with four fields; focus centrally located ..... *Prosopium williamsoni*
(figure 3, b)

6. a) Primary radii on both posterior and anterior fields ..... Catostomidae
(also includes the cyprinid genera *Rhinichthys* and *Orthodon*; figure 3, c)

b) Primary radii absent on either anterior or posterior field 7

7. a) Primary radii present on anterior field, but absent on posterior field 8

b) Primary radii absent on anterior field, but present on posterior field .....
..... Cyprinidae
(figure 4, a)

8. a) Far fewer circuli in lateral than in anterior field ..... Cyprinodontidae
(figure 4, b)

b) Number of circuli in lateral field approximately equal to number in anterior field ..... *Embiotocidae*
(specifically *Hysterocarpus traskii*; figure 4, c)

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I wish to express my thanks to Mr. W. I. Follett and Mrs. L. Dempster of the California Academy of Sciences for their advice and cooperation and to Dr. W. G. Kinzey, City University of New York, for his support and encouragement during the initial phases of this work. My thanks also to Dr. R. W. Brocksen and Messrs. L. Courtois, W. Wurtsbaugh, and H. W. Li, Department of Animal Physiology, University of California, Davis; to Mr. Lyons, U. S. Department of Reclamation; and to Messrs. A. Calhoun, L. Fisk, E. Armstrong, M. Coots, E. P. Pister, R. Reavis, and J. Burns, California Department of Fish and Game, for their aid in obtaining specimens. I also appreciate the helpful criticisms of the manuscript given by Mr. W. I. Follett, California Academy of Sciences; Dr. D. L. True, Department of Anthropology, University of California, Davis; and Dr. J. D. Hopkirk, Department of Biology, Sonoma State College. Finally, my thanks go to my wife for her help during all phases of this project.

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PLEISTOCENE FISHES FROM ALAMEDA COUNTY, CALIFORNIA

By RICHARD W. CASTEEL and DAVID P. ADAM, Menlo Park, Calif.

Abstract.—Six types of freshwater fishes were recovered from an early Pleistocene (Irvingtonian) locality on the east side of San Francisco Bay, Alameda County, Calif. The fauna includes one centrarchid, one salmonid, three cyprinids, and one catostomid. The fauna indicates fluvial and slow-moving or lacustrine aquatic environments. One of the cyprinids and the catostomid are assigned to provisional genera because of the inadequate amount of material available for study and the obvious differences between these fossils and known fossil or recent fishes. They are new additions to the Pleistocene fish fauna of California. Paleogeographic distribution of some of these fishes indicates former fluvial or lacustrine connections between Utah, Idaho, Oregon, Washington, Nevada, and California. The Pliocene and Pleistocene fossil fish faunas indicate the widespread occurrence of genera now endemic to California. A similar picture is presented by the molluscan evidence.

This paper describes the remains of six freshwater fishes (including two new provisional genera) from the vicinity of Oak Knoll Naval Hospital, Oakland, Alameda County, Calif. (fig. 1) (37°45′45″ N., 122°8′32″ W.), on the east side of San Francisco Bay.

The fishes occur in a deposit of gravel, sand, silt, and clay that overlies and contains pebbles of the Pliocene(?) Leona Rhyolite (Radbruch, 1969, p. 4 of text). The beds are poorly defined and have been tilted and contorted. The Oak Knoll locality is in a small ridge that has produced a faunal assemblage (USGS vertebrate loc. M–1242 and UCMP loc. V–5834) of probable early Pleistocene (Irvingtonian land mammal) age. These localities are shown as Pleistocene locality 22133 on Radbruch's (1969) map. The remains of a freshwater fish, *Orthodon* sp., were described from UCMP loc. V–5834 (Casteel and Hutchison, 1973) and were found in association with the remains of amphibians (*Rana*, *Taricha*), reptiles (*Clemmys*, Colubridae), birds, and mammals (Sciuridae, *Microtus*, *Odocoileus*, *Equus*, ?Proboscidea) that indicate Irvingtonian age.

Two of the fossils are new to the fossil record for California; most, however, are represented in the recent endemic freshwater fish fauna of California. The two new genera are clearly different from existing members of their families, as well as from the known fossil members. At the present time, however, each is known only from a single diagnostic element. Since it it not apparent that species may be separated on the basis of differences in these elements, we have chosen to refer them to provisional genera (α and β) within their respective families. These provisional genera are presented here for the purpose of description. We hope that with the analysis of additional material it will be possible to establish valid specific and (or) generic taxa for these specimens.

The additional material from USGS vertebrate loc. M–1242, as well as the previously undescribed material from UCMP loc. V–5834, indicates a much richer fish fauna than that previously described.

FOSSIL MATERIAL

Family SALMONIDAE

Salmo(?) sp.

Figure 2*B*

Referred material.—UCMP 112742, one nearly complete thoracic vertebra 3.0 millimetres wide.

The vertebra clearly represents a salmonid (*Salmo*, *Salvelinus*, or *Oncorhynchus*) because of the characteristic netlike patterning of its outer surfaces. The specimen is not representative of the genus *Oncorhynchus*, on the basis of the relative sizes of the pores and the intensity of the ribbing on the lateral surface. As it is not possible, with the material available, to distinguish between the thoracic vertebrae of the genera *Salmo* and *Salvelinus* for individuals with vertebrae the size of the specimen in question, the specimen is provisionally assigned to the genus *Salmo*.

This appears to be the first fossil record of this genus or of any salmonid of Irvingtonian age from central California.

Family CYPRINIDAE

Genus α

Figure 3*D–F*

Referred material.—USNM 184077, a right dentary collected by D. P. Adam in April 1972.

Diagnosis.—A cyprinid fish characterized by distinc-

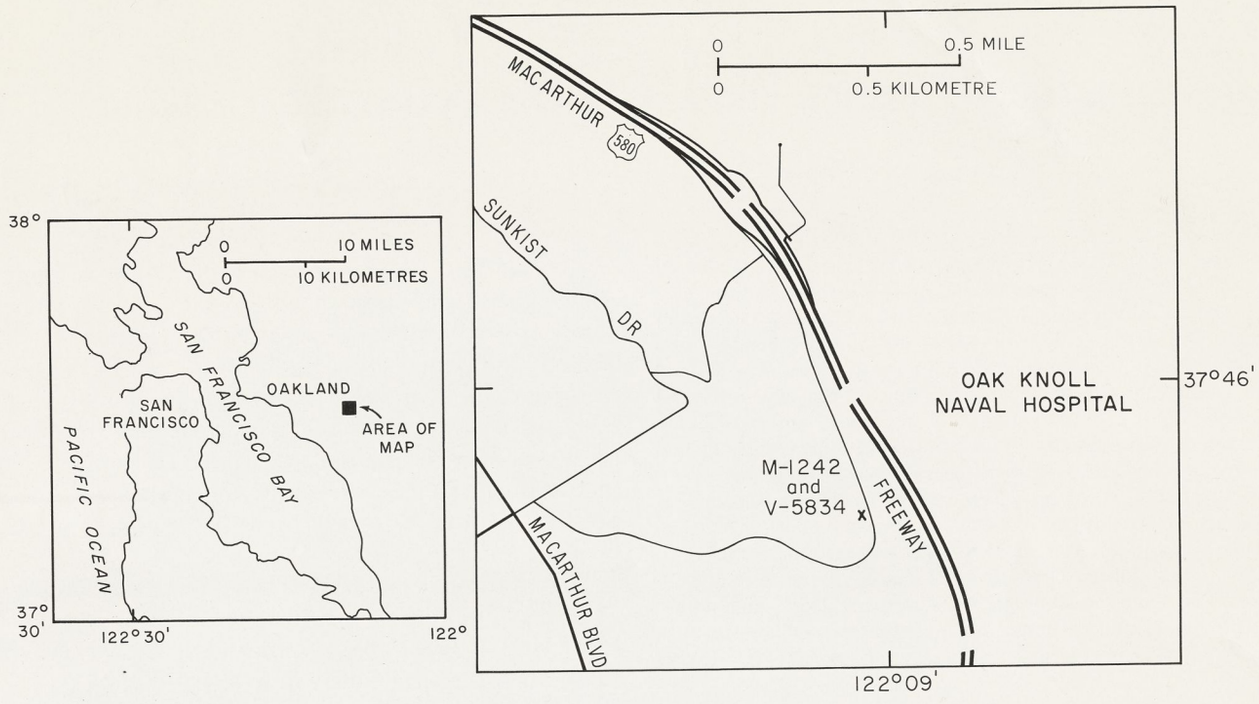

FIGURE 1.—Location of USGS vertebrate loc. M–1242 and University of California Museum of Paleontology loc. V–5834, Oakland, Alameda County, Calif. Base from U.S. Geological Survey Oakland East, 1959; photorevised, 1968.

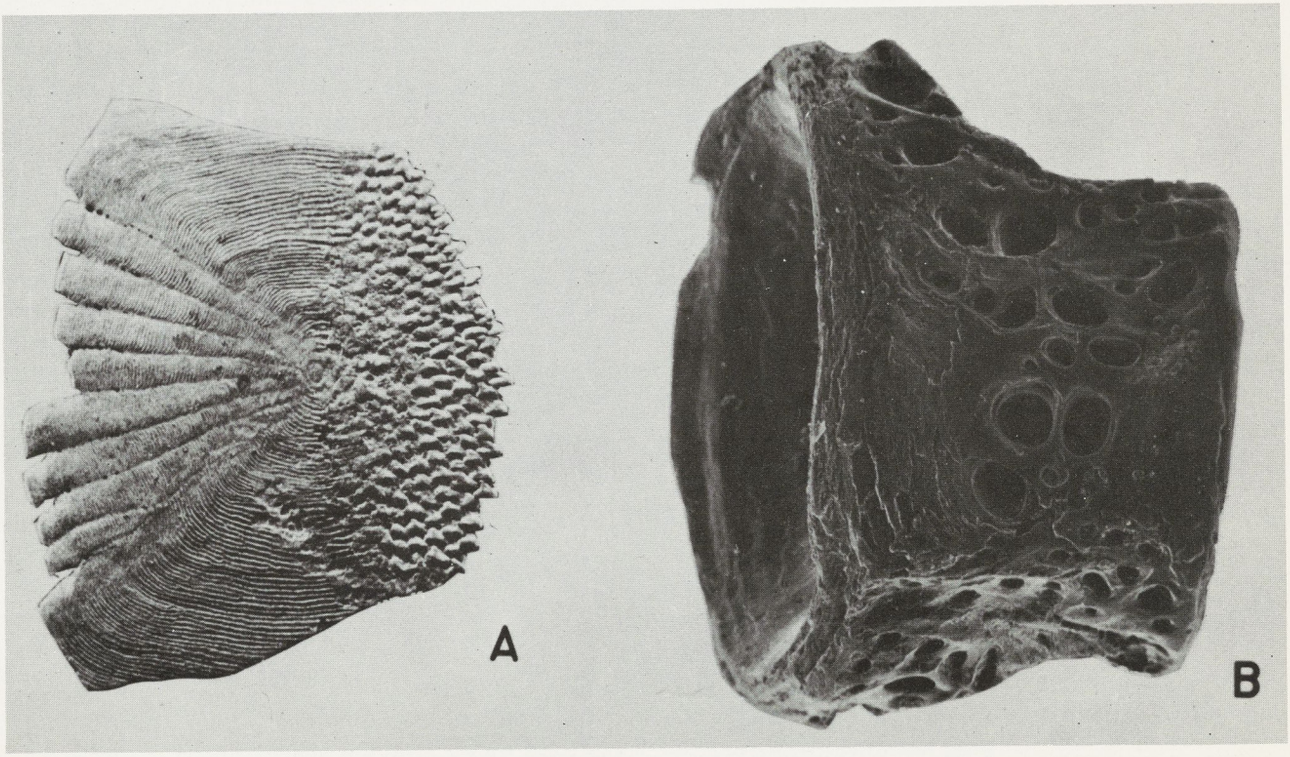

FIGURE 2.—Scanning electron micrographs. *A*, Scale of *Archoplites* cf. *A. interruptus* (Girard); × 25; anterior field to left; U.S. National Museum 184081. *B*, Thoracic vertebra of *Salmo*(?) sp.; × 32; UCMP 112742.

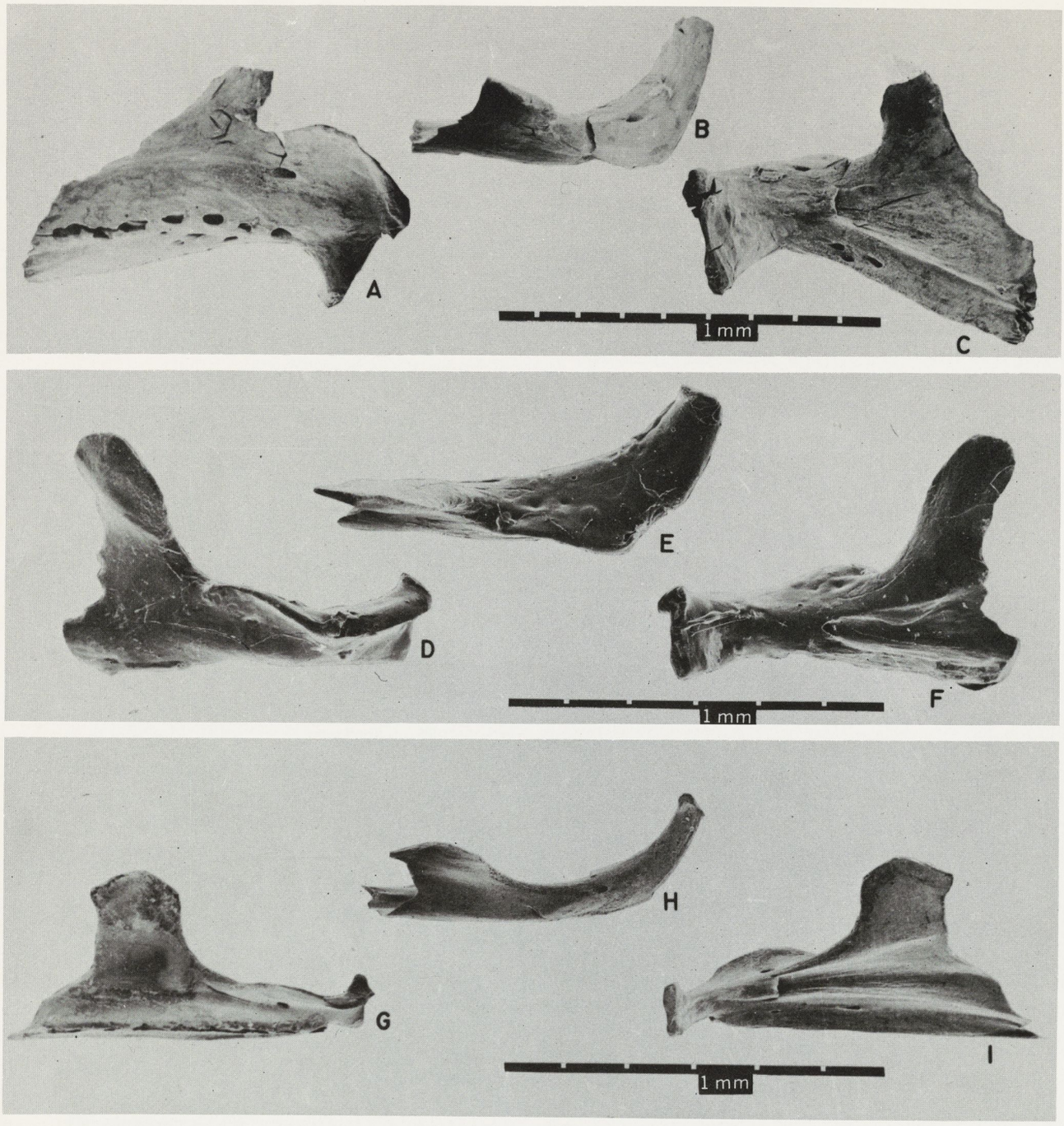

FIGURE 3.—Scanning electron micrographs of right dentaries of three species of crypinids. *A–C*. Right dentary of *Aerocheilus alutaceus* Agassiz and Pickering; specimen 5953. *D–F*, Right dentary of genus *a*; USNM 184077. *G–I*, Right dentary of *Orthodon microlepidotus* (Ayres); specimen 5084.

tive lipping of the dorsolateral margin of the dentary. The dentary is relatively short and very robust. The flange along the dorsolateral surface is oriented dorsally just anterior to the ascending process and then curves laterally toward the anterior and recurves ventrally at the anterior end of the dentary. The ascending process is nearly perpendicular to the long axis of the dentary, and there is a strongly developed symphyseal knob at the anterior end of the dentary.

The specimen is a nearly complete right dentary, lacking the ventral margin and the pores of the anterior part of the preoperculomandibular sensory ca-

nal. A part of the thin posterior margin of the dentary is also probably lacking. The dentary is 6.1 mm long, the symphyseal knob is 1.4 mm high, and the ascending process is 4.3 mm high. The general form of this dentary is not comparable with any of the recent native freshwater cyprinids of California; however, it appears to be matched by a large series of fossil dentaries from Idaho deposits of Pliocene or Pleistocene age in the possession of G. R. Smith (R. R. Miller, written commun., Feb. 10, 1975).

For comparison, figure 3 illustrates the dentary of genus α (fig. 3*D–F*) and the right dentaries of *Orthodon microlepidotus* (Ayres) (fig. 3*G–I*) and *Acrocheilus alutaceus* Agassiz and Pickering (fig. 3*A–C*). As noted by Hopkirk (1974, p. 63), *O. microlepidotus* is characterized by "dorsolateral surface of dentary (anterior to ascending process) strongly flanged and sharp-edged to produce the semi-truncate lower jaw."

The genus *Acrocheilus* is characterized by a highly modified dentary. In this genus the dentary is extremely shortened and robust, and is characterized by a marked development of the flange on the dorsolateral and dorsoanterior margins. The genus is known from fossil material (*A. xestes*) from a fluviatile facies of the Glenns Ferry Formation of late Pliocene and early Pleistocene age in Idaho (Miller and Smith, 1967). This formation also contains a number of freshwater fish presently endemic in the Sacramento–San Joaquin and Salinas–Pajaro drainages in California (Miller and Smith, 1967; Miller, 1958, 1965; Uyeno, 1961). However, genus α does not approach *Acrocheilus* in the extreme degree of its modification (fig. 3). Likewise, the development of the flange along the dorsolateral surface, the sinuous line of this flange, ranging from a dorsal to a ventrolateral orientation, the curvature of the dentary as seen in dorsal aspect, and the robust nature of the dentary itself separate genus α from *Orthodon*, as well as from the other California cyprinids.

Mylopharodon cf. *M. concephalus* (Baird and Girard)

Referred material.—USNM 184078 consists of one left pharyngeal bone and a pharyngeal bone fragment with the anterior edentulous process and last tooth socket, one right pharyngeal bone fragment with the posterior edentulous process and the first two tooth sockets, one molariform pharyngeal tooth (probably III), one fragment of the basioccipital consisting of the posteriorly projecting process, and the masticatory process of the basioccipital.

At the present time this genus is monotypic and is represented by *M. conocephalus* (Baird and Girard), endemic to the California freshwater fauna. This species has been recorded from a fossil assemblage at Potter Creek Cave, Shasta County, Calif., and assigned a Pleistocene (Wisconsin) age (Sinclair, 1904; Jordan, 1907; Uyeno, 1961; Uyeno and Miller, 1963). Other fossil remains of the genus *Mylopharodon* include *M. hagermanensis* and *M.*(?) *condonianus* from Pliocene or Pleistocene Lake Idaho (Miller and Smith, 1967; Uyeno, 1961; Cope, 1883; Miller, 1965). The age of the Lake Idaho fauna is placed at 3.0—3.5 million years (Linder, 1970; Linder and Koslucher, 1974; Miller and Smith, 1967; Evernden and others, 1964).

Orthodon cf. *O. microlepidotus* (Ayres)

Referred material.—USNM 184079, UCMP 77454. A fragment of the posterior edentulous process of a left pharyngeal bone containing the base of pharyngeal tooth I and 115 isolated pharyngeal teeth represent this species.

At the present time the genus *Orthodon* is monotypic, with the single species, *O. microlepidotus* (Ayres), endemic to California. The genus has been reported from fossil freshwater assemblages from central California and the San Francisco Bay area ranging in age from Hemphillian (Pliocene) to Rancholabrean (late Pleistocene) (Casteel and Hutchison, 1973). Remains of this species have also been recovered from Pliocene or Pleistocene lacustrine facies of the Cache Formation of Anderson (1936) near Clear Lake, Lake County, Calif. (Casteel and Rymer, 1975).

Family CATOSTOMIDAE

Genus β

Figure 4*A–D*

Referred materials.—USNM 184080 consists of a complete first vertebra 2.6 mm wide and 2.6 mm high, a complete first vertebra 2.0 mm wide and 2.0 mm high, and a fragment of the left half of a first vertebra collected by D. P. Adam in April 1972. UCMP 112743 consists of two complete first vertebrae 2.5 and 1.9 mm wide and 2.5 and 2.0 mm high, respectively.

Diagnosis.—A catostomid fish characterized by a convex projection of the dorsal and dorsolateral margins of the anterior face of the first vertebra. The dorsolateral surfaces contain a pair of pits for the ventral articulating projections of the scaphia (Nelson, 1948), and the ventrolateral surfaces have rudimentary, laterally projecting transverse processes characteristic of the first vertebra of the catostomids native to western North America.

The first vertebra of genus β possesses relatively large dorsal pits for articulation with the scaphia, as well as rudimentary, laterally projecting transverse processes on the ventrolateral surfaces. The dorsal half

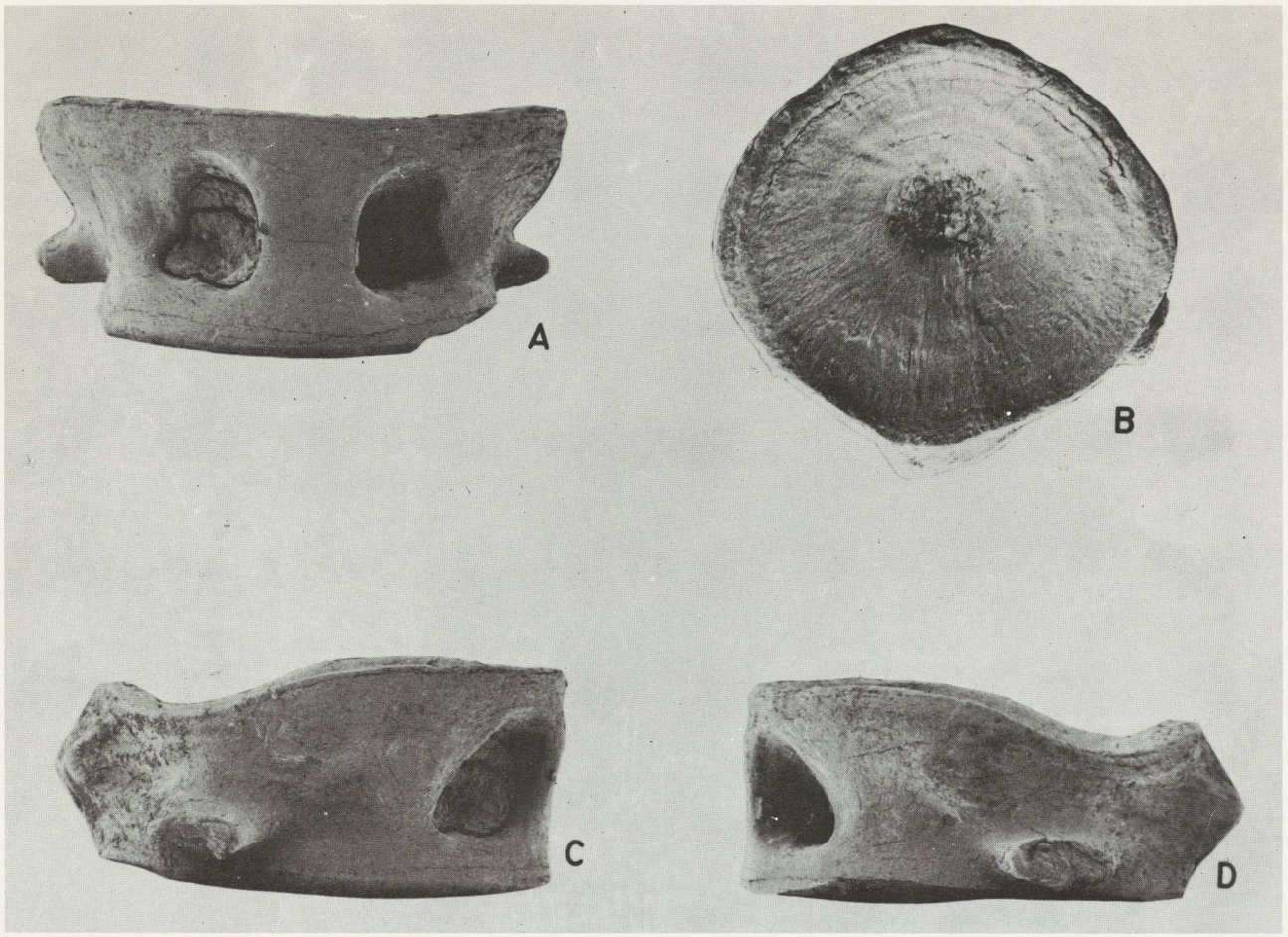

FIGURE 4.—Scanning electron micrographs of first vertebra of genus β; USNM 184080; × 18. *A*, Dorsal aspect. *B*, Posterior aspect. *C*, Left lateral aspect. *D*, Right lateral aspect.

of the anterior margin of the vertebra is markedly convex. The posterior face is flat in lateral view.

Figure 4 illustrates the first vertebra of genus β in dorsal, anterior, and left and right lateral aspects. The occurrence of stublike or rudimentary transverse processes of relatively small diameter on the first vertebra is common among the catostomids native to western North America. The first vertebra of the native catostomids in western North America is presently characterized by anterior and posterior faces that are relatively parallel, and the centrum is relatively thin anteroposteriorly. In contrast, the first vertebra of genus β is more robust, less elongated dorsoventrally and has anterior and posterior faces that are not roughly parallel.

Attempts to identify features similar to those of genus β among other members of the Ostariophysi native to North America have proven fruitless. The closest analog appears among the members of the Catostomidae. It was not possible, however, to establish criteria that could place the specimen unquestionably in one of the three existing genera of catostomids native to California (*Catostomus*, *Chasmistes*, or *Xyrauchen*). Therefore, the genus β was established to reflect the affinities of this material to the Catostomidae, and yet indicate its distinction from the three existing genera of this family native to California.

Family CENTRARCHIDAE

Archoplites cf. *A. interruptus* (Girard)

Figure 2*A*

Referred material.—USNM 184081 consists of numerous ctenoid scale fragments characteristic of *A. interruptus* (Girard) (Casteel, 1972), two fragments of the anterior part of the dentary (one left, one right), one dentigerous fragment of either a premaxillary or a dentary, one first vertebra 2.4 mm wide, one second vertebra 2.3 mm wide, three thoracic vertebra 3.2, 2.1, and 2.2 mm wide, one caudal vertebra 2.0 mm wide,

and one ultimate vertebra 2.0 mm wide. UCMP 113313 consists of one fragment of the anterior articular process of a left operculum and UCMP 113312 is a proximal fragment of a dorsal pterygiophore.

The genus *Archoplites* is represented by a single extant species, *A. interruptus* (Girard), which was restricted to the inland waters of California prior to its introduction by man outside that range (La Rivers, 1962; Moyle and others, 1974; McCarraher and Gregory, 1970).

The genus has been reported as a fossil from the early or middle Pleistocene at Moses Lake, Wash. (Miller, 1965), from Pliocene or Pleistocene Lake Idaho as *A. taylori* (Miller, 1965; Miller and Smith, 1967), and from a late Pleistocene locality near Sacramento, Calif., dated at 103,000 before present (Hansen and Begg, 1970) as *Archoplites* sp. A scale of this genus has also been identified from lacustrine facies of the Pliocene or Pleistocene Cache Formation near Clear Lake, Lake County, Calif. (Casteel and Rymer, 1975).

INDETERMINATE REMAINS

In addition to the above material, the following fish remains (USNM 184082) were also recovered: Indeterminate pterygiophores, indeterminate spiny rays, fragmentary cyprinid pharyngeal arches and teeth, two fragments of the first vertebra of an indeterminate cyprinid, numerous thoracic and caudal vertebrae (ranging in width from 1–3 mm) from indeterminate small cyprinids and (or) catostomids, an indeterminate cyprinid ceratohyal, two cyprinid opercular fragments (one left, one right) each consisting of the opercular arm and the articular process, and numerous scale fragments.

DISCUSSION

This fossil fish fauna probably represents a fluvial and slow-moving or lacustrine aquatic environment. *Archoplites interruptus*, *Orthodon microlepidotus*, and *Mylopharodon conocephalus* presently are found in environments that range from large, sluggish creeks, small rivers, and the upper reaches of large rivers in the Upper Sonoran Life Zone to the fast- and slow-moving and standing waters in the Lower and Upper Sonoran Life Zones (the sucker and hitch zones, respectively, of Hopkirk, 1974). Since none of the remains show marked signs of stream abrasion, it may be assumed that the cyprinid genus α and the catostomid genus β were also inhabitants of this environment and do not represent members of faunas whose remains were deposited after extensive transport. The occurrence of *Salmo*(?) could be interpreted as indicating permanent, cold headwater creeks. However, since this genus presently migrates through all water types, from headwater areas to the open sea, its presence in the Oak Knoll assemblage is not unlikely. It does indicate that active contact did exist between streams of the Transition, Canadian, and (or) Hudsonian Life Zones and the waters in the area of the Oak Knoll Naval Hospital.

The paleogeographic distribution of some of these fishes indicates a close relation between the fish faunas of the Central Valley of California and the fossil fish faunas of Idaho and eastern Washington. *Archoplites* and *Mylopharodon*, both presently endemic to central California, have also been identified in Pliocene or Pleistocene deposits in Idaho and Pleistocene deposits in eastern Washington. Other genera (*Ptychocheilus*, *Chasmistes*, *Acrocheilus*, *Catostomus*) from the Pliocene or Pleistocene Idaho fish faunas indicate former connections with the Colorado, Columbia–Snake, Sacramento–San Joaquin, and Klamath River systems, as well as with lake systems in the Great Basin. A similar pattern, involving the disjunct distributions of the mollusks *Pisidium ultramontanum* Prime, *Ceriphasia acutifilosa* (Stearns), *Carinifex newberri* (Lea), *Valvata utahensis*, *Stagnicola utahensis*, and *Pyrgulopsis* spp., has been described by Taylor (1960). Their distributions appear to extend from Walker Lake, Nev. across Eagle Lake, the upper Pit River, Calif., to Klamath Lake, Fossil Lake, and the Malheur basin, Ore., to the Snake River in southern Idaho and western Wyoming, Gentile Valley and Bear Lake, southeastern Oregon, and, finally, to Utah Lake, Utah. The period of time assigned to these widespread, though not necessarily coeval, connections ranges from Pliocene to early Pleistocene (Taylor, 1960, p. 332).

These disjunct distributions imply an earlier sharing of fish faunas between the major river systems in the West and draw attention to the areas of interior drainage in southeastern Oregon that formerly drained into the Pacific Ocean (Russell, 1903) and parts of the northern and western Great Basin, as well as to questions concerning the course of the pre-Pleistocene ancestral Snake River (Miller, 1965).

The age of the Oak Knoll material is Irvingtonian (early Pleistocene) (Radbruch, 1969; Casteel and Hutchison, 1973). The fish remains indicate species that range from Pliocene through late Pleistocene (Hemphillian through Rancholabrean land mammal ages).

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INFERRED HOLOCENE TEMPERATURE CHANGES IN THE NORTH COAST RANGES OF CALIFORNIA*

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ABSTRACT

The remains of fish scales from two sediment cores taken in Clear Lake, California have been used to estimate the sizes of fish at various points in time over the last ≈12,000 years. Since growth rates of fish are primarily temperature-dependent, their patterns of growth constitute a valuable climatic response record reflecting variations in temperature.

*Publication approved by the Director, U.S. Geological Survey.

INTRODUCTION

The patterns of growth reconstructed from fish scales may provide sensitive climatic response records, indicating fluctuations in temperature. Fish are poikilotherms and their metabolic rates vary positively with the temperature of their environment. Their vital processes are generally accelerated by warmer temperatures and decelerated by cooler ones (Alexander 1967, Lagler et al. 1962). In temperate regions fish also undergo seasonal fluctuations in growth rates. These seasonal pulses in growth are recorded in bones and scales as annuli (Chugunova 1959, Ovchynnyk 1962, McKern et al. 1974) (Figure 1). Appropriate fish remains can be used to identify type of fish, to

Figure 1 near here

reconstruct its size at the end of each year of growth, and, where these data are available for a long period of time, to infer changes in temperature.

METHODS

This method was first applied to the materials recovered from a series of eight sediment cores taken from Clear Lake, California by the U.S. Geological Survey (Sims 1974). Fish remains from two of these cores have been analyzed. The two cores (numbers 6 and 7) are from the Oaks and Highlands Arms of Clear Lake, respectively (Figure 2). The total number of scale remains from the

Figure 2 near here

samples of these two cores is 1580. All scales were mounted in glycerine jelly and identified. From this total approximately 85 percent were identified as belonging to *Hysterocarpus traski* Gibbons (Tule perch), an embiotocid native to Clear Lake (Hopkirk 1974, Casteel 1972). The scales of

this species were then examined to determine which showed adequate annuli for growth reconstructions. A total of 255 Tule perch scales from both cores were found to be suitable. The annuli were identified on these scales and measurements of the antero-lateral radius from the nucleus to each annulus were made (Figure 1). The standard lengths (in mm) of the fish at each annulus or year of growth were determined from these radial measurements using the regression of standard length on scale radius established from recent specimens of this species. Details of these procedures, as well as the basic data have been presented elsewhere (Casteel et al. 1975, 1977, 1977).

RESULTS

Analysis of the fish scales from Core 7 indicated a period of depressed temperatures between ≃9000 and 10,000 BP followed by a relatively steady increase in temperature which peaked between ≃4000 and 2800 BP. The data indicated a period of decreasing temperature since ≃2800 BP (Casteel et al. 1977). The data from Core 6 indicated the same pattern of temperature change over the last ≃11,000 years. Results for the last 3000 years, however, differed between age class 1 and age classes 2 and 3. The former indicated a period of increasing temperature since ≃1800 BP, whereas the latter indicated rising temperatures between ≃3000 and 1800 BP, followed by a steady and marked decline in temperature (Casteel et al. 1977).

Under the assumption that the records from these cores should be responding to the same general climatic influences of increasing or decreasing temperature, the results of the two independent studies have been combined. The mean standard lengths for each slug from Cores 6 and 7 were plotted against the mean ages for these slugs as determined from estimates of the rates of sedimentation in the relevant Holocene parts of each core. The data were partitioned according to age classes. Only the data for age classes 1

through 3 were examined because those for age classes 4 through 6 were based upon extremely small sample sizes and highly subject to random variations. Since these latter age classes constitute only 9 percent of the available data, their exclusion was believed to be justified.

Figure 3 illustrates the result of combining the data from Cores 6 and 7.

Figure 3 near here

The general pattern is one of increasing temperature in the North Coast Ranges from ≈12,000 to 3000 BP, followed by a general decline in temperature toward the present. Although this pattern is probably least apparent in age class 1 (Figure 3A), a runs test indicates a significant time trend in the data ($\alpha = .05$) (Siegel 1956). The mean standard lengths for all three age classes were tested against their representative averages for the entire ≈12,000-year period using a χ^2 test and all were found to show significant non-random patterning ($\alpha < .01$).

CONCLUSIONS AND DISCUSSION

Data for age class 3 probably reflect best the climatic or temperature response record. Here temperature is increasing between ≈12,000 and 8000 BP. This is followed by a period of decreasing temperatures lasting until ≈5000 BP. Temperatures then begin to rise to their Holocene zenith between ≈5000 and 3000 BP, after which they decline toward the present.

While these results diverge somewhat from the general model of post-Pleistocene temperature/precipitation change for western North America (Antevs 1952, 1955, Bryan and Gruhn 1964), they match relatively well with more recent data concerning the termination of the Altithermal and marked cooling since 1000 BP as determined from studies of bristlecone pine in the White Mountains of

California (LaMarche 1973, 1974), as well as in Nevada (LaMarche and Mooney 1967). The results are consistent with those of Adam (1967) and Heusser (1960) and with estimates of the onset of Neoglacial conditions in the Sierra Nevada and California generally by Porter and Denton (1967). Generally, the time period from 2510 to 2760 BP has been seen as a time of increased precipitation and/or decreased evaporation in the Northern hemisphere and a major warming change is said to have occurred between 4230 and 4240 BP (Wendland and Bryson 1974). These same authors also argue for a probable climatic change between 5900 and 6050 BP (Wendland and Bryson 1974, Denton and Karlén 1973). This coincides with the period of mid-Holocene temperature depression indicated in Figure 3.

Finally, a recent study of Holocene changes in the water level of Lower Klamath Lake, located approximately 320 km north-northeast of Clear Lake, has indicated periods of high lake level at 4200 to 6000 BP and 600 to 1000 BP, with low lake levels between 1000 and 4200 BP (Grayson 1976a,b). These periods of high lake stands coincide very well with periods of decreased temperature indicated in Figure 3. This is also true for the mid-Holocene period of low lake level and the high temperatures indicated in Figure 3. Such an inverse relationship between temperature and precipitation is characteristic of the Köppen-Geiger Csb climates with marked summer/dry and winter/wet seasons (Strahler 1965, Trewartha et al. 1967). This same pattern was earlier proposed by Martin (1963) with regard to increased Altithermal aridity in California.

These results indicate that the use of fish scales may well provide a further means of inferring temperature changes and thus allowing for a discussion of Holocene temperature change without the need to consider both temperature and atmospheric moisture simultaneously (Deevey and Flint 1957).

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List of Figures

Figure 1. Scale of *Hysterocarpus traski* Gibbons (Specimen 136-13) from Core 7 showing measurement of antero-lateral radius to first (R_1) and second (R_2) annuli (x20). Anterior field of scale is to the viewer's left.

Figure 2. Map of Clear Lake, California study area showing locations of Cores 6 and 7 in the Oaks and Highlands Arms, respectively.

Figure 3. Estimated size (standard length in mm) of *Hysterocarpus traski* Gibbons. Ordinate, estimated mean standard lengths in mm; abscissa, mean age of samples in ^{14}C years BP. A, age class 1; B, age class 2; C, age class 3. Temperature change during this period is inferred to have followed a similar pattern.

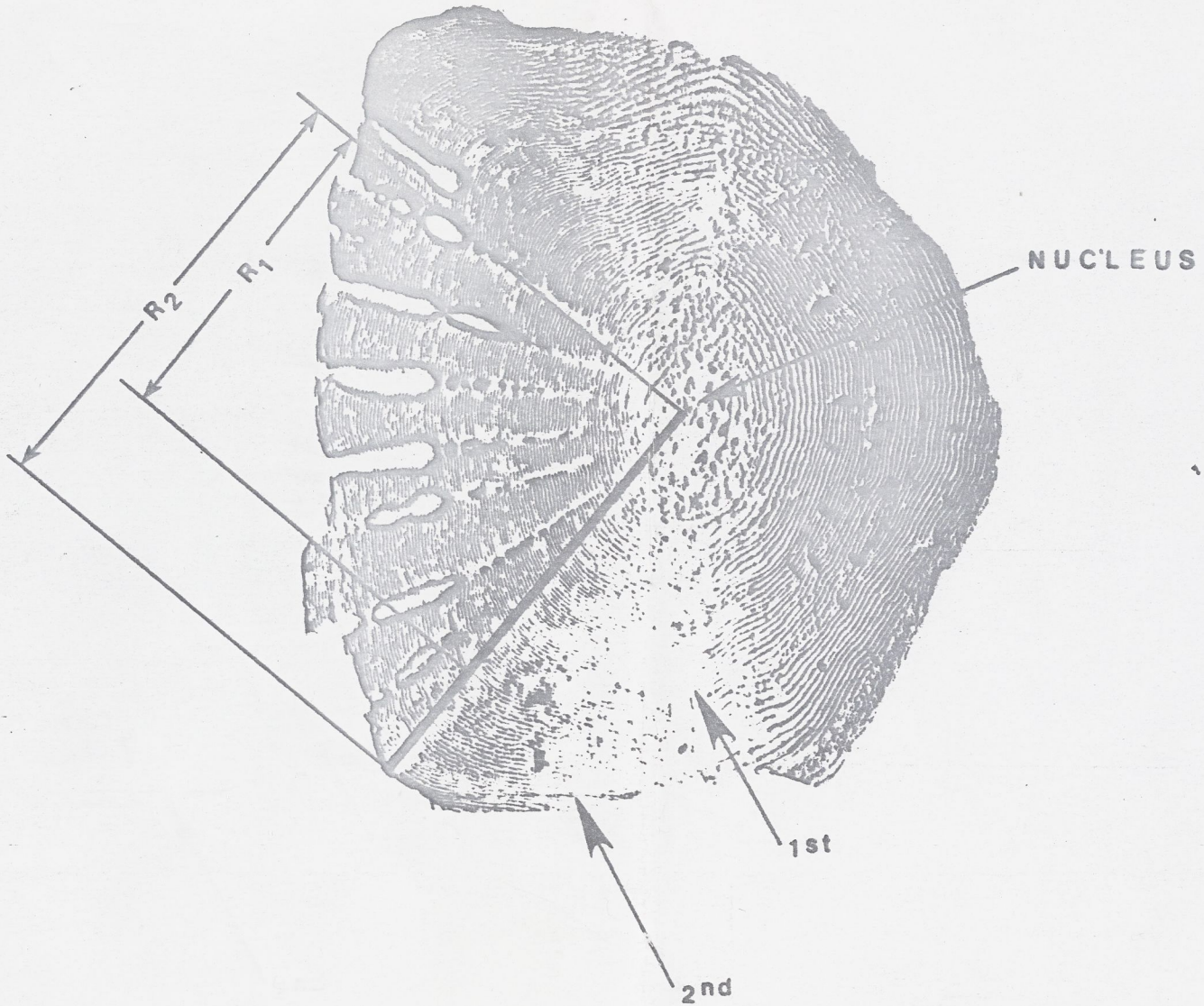

Figure 1

Figure 2

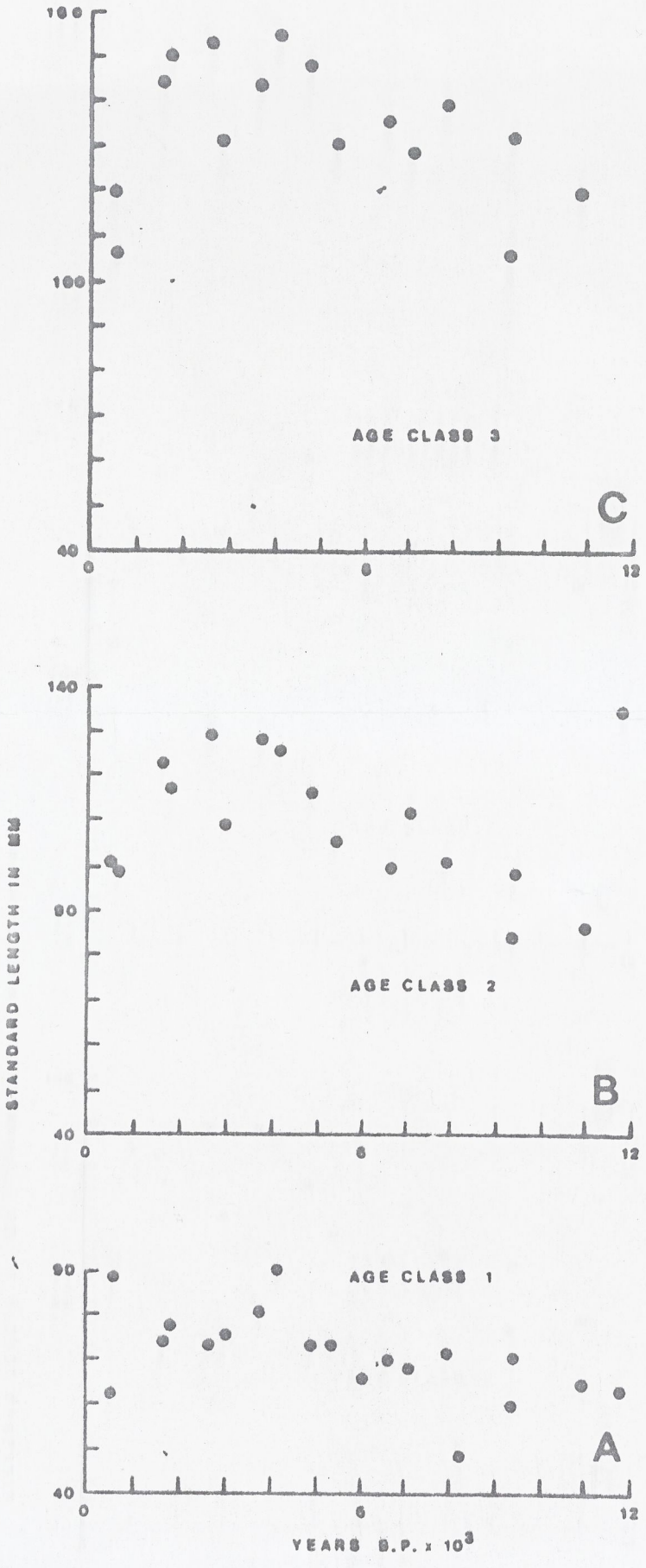
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Figure 3

The Great Basin Naturalist

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LIFE HISTORY OF THE CUI-UI, *CHASMISTES CUJUS* COPE, IN PYRAMID LAKE, NEVADA: A REVIEW

William F. Sigler[1], Steven Vigg[2], and Mimi Bres[3]

ABSTRACT.—The cui-ui, *Chasmistes cujus* Cope, a member of the sucker family and endemic to Pyramid Lake, Nevada, is listed as endangered by the U.S. Fish and Wildlife Service. Cui-ui was once a major source of sustenance for native Americans, who have inhabited the Lahontan region for at least 11,000 years. The Northern Paiutes developed sophisticated fishing technology to harvest this resource. The original distribution of cui-ui was the ancient Lake Lahontan complex, but as a result of climatic changes it was restricted to the Pyramid-Winnemucca-Truckee system by the turn of the 20th century. Transbasin water diversions (1905 to present) have resulted in further restrictions of habitat. The species is now limited to Pyramid Lake and the lower Truckee River. Reproduction is from hatcheries as well as limited natural reproduction. Females produce more than 40,000 2–mm eggs per year. The normal development is described from the unfertilized egg through 912 hours post-hatching, when the fry are actively feeding and approaching adult body form. The unusual feature of adult cui-ui morphology is the relatively large ventro-terminal mouth, with thin and obscurely papillose lips. Cui-ui grow slowly and may live 18 years or possibly much longer; females generally live longer and attain a greater size than males. The highest adult mortality probably occurs during spawning runs. At this time they are vulnerable to predation, stress, and sometimes environmental degradation. The highest larval mortality probably occurs from predation when they are planted or migrate into the lake. The trophic ecology of the species is poorly understood, but they are known to ingest algae and zooplankton. Spawning behavior is documented. At present, natural reproduction is probably still the limiting factor for the cui-ui population. Cui-ui composed less than one percent of the total fish in Pyramid Lake during 1975–1977. During 1982 the largest cui-ui spawning run (13,000) in recent years occurred. The activity of cui-ui in the lake closely resembles that of the Tahoe sucker being most active during the spawning season each spring. Cui-ui inhabit the inshore-benthic zone and the pelagic waters of Pyramid Lake (<46 m).

The cui-ui, *Chasmistes cujus* Cope, a member of the sucker family (Catostomidae), is present only in Pyramid Lake and the affluent lower Truckee River, Nevada (Fig. 1). Because of its limited range and depleted numbers, it is listed as endangered (Federal Register, Vol. 32/48, 11 March, 1967). Cui-ui until recently was an important food source for Northern Paiute, the native Americans who have inhabited the region for at least 11,000 years. Prehistorically the habitat of cui-ui consisted of the Lake Lahontan system, which reached its maximum size of about 22,300 km^2 some 13,000 years before present (BP) and inundated a large portion of northwestern Nevada. The cui-ui was present in Winnemucca Lake until the late 1920s or early 1930s (Fig. 2).

There is general agreement that the ecological devastation of the cui-ui's lake and river environment was caused in part by the Newlands Reclamation Irrigation Project (NRIP), which was authorized by the U.S. Congress in 1903. In 1905 Derby Dam was dedicated, and

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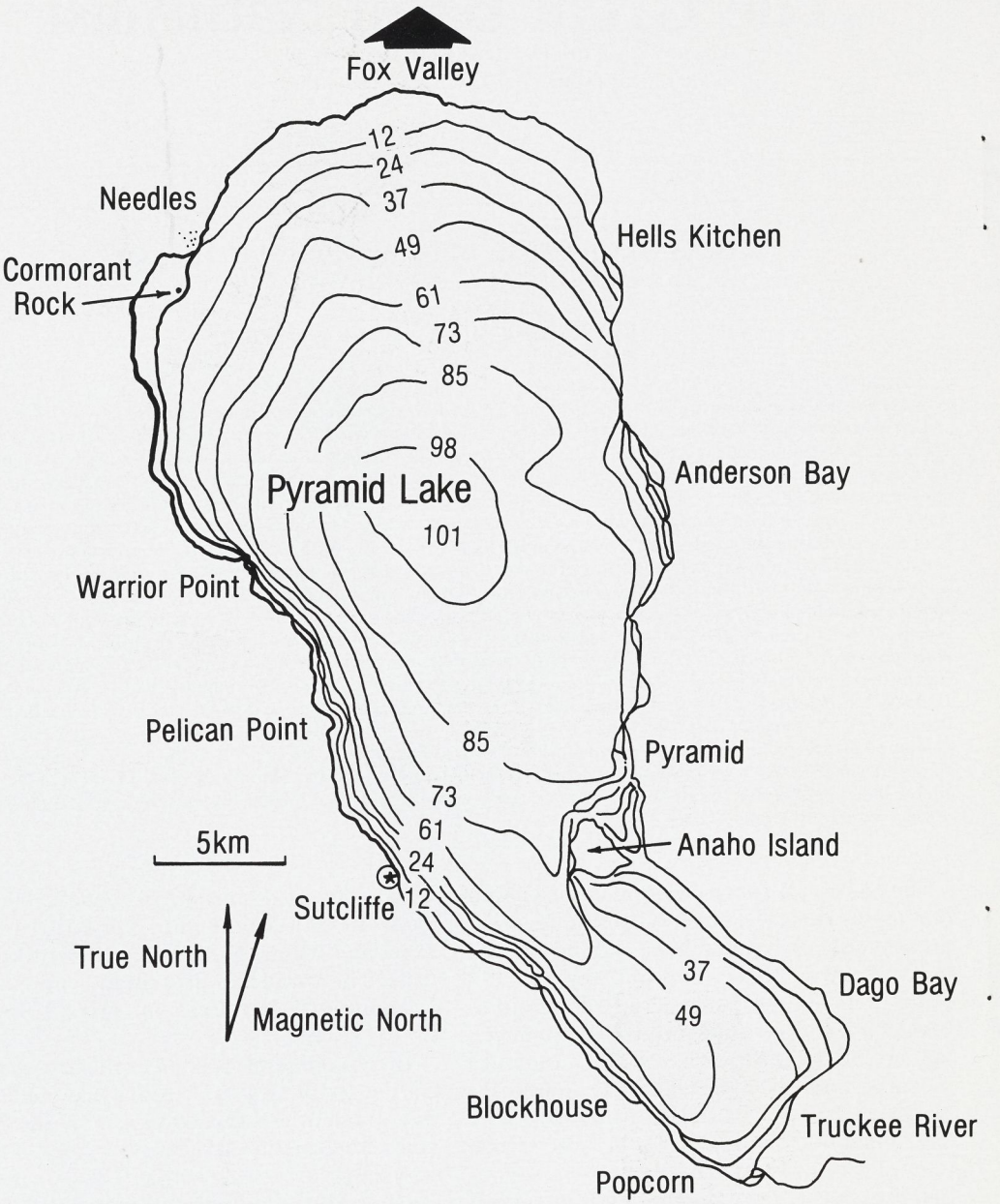

Fig. 1. Bathymetric map of Pyramid Lake, Nevada; depth contours are in meters at elevation 1154.9 m.

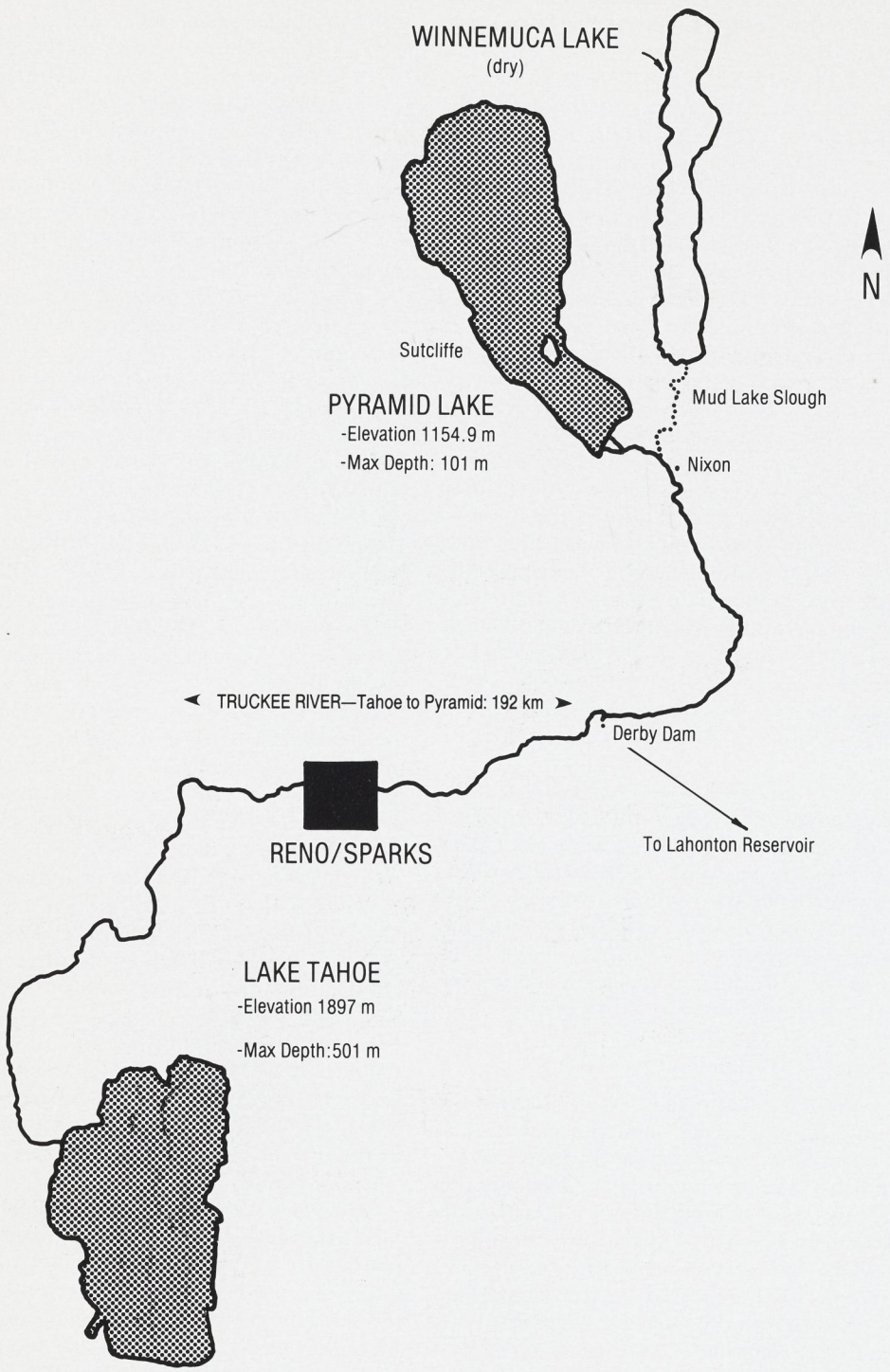

Fig. 2. The Truckee River–Pyramid Lake Ecosystem.

transbasin water diversion from the Truckee River to the Carson River system began. Lahontan Dam on the Carson River was completed in 1915, creating Lahontan Reservior—the water storage impoundment for the NRIP. From 1915 to 1970 as much as half or more of the total flow of the lower Truckee River was diverted to the NRIP. Because of droughts and diversions, the level of Pyramid Lake declined more than 24.4 m from 1909 to 1968, Pyramid Lake increased in total dissolved solids (TDS) from about 3500 to 5500 mg/l, and Winnemucca Lake disappeared in 1938. A delta developed at the mouth of the Truckee River in the early 1930s that was virtually impassable to spawning migrations of cui-ui. Natural reproduction in the Truckee River was very limited for about 50 years (until the new Marble Bluff dam and the fishway became functional for cui-ui in 1982). However, during years of exceptionally high flow, natural reproduction may have been possible. Upstream, Siphon dam (washed out in 1958), and about 1 mile below it the original Marble Bluff dam (washed out in 1950) were also barriers to migrating cui-ui. Neither of these obstructions had functional fish ladders. The original Numana Dam also barred cui-ui migration.

It is our objective to synthesize information collected during the Pyramid Lake Ecological Study, conducted by W. F. Sigler & Associates Inc. during 1975–1978, with available data from agency reports and research publications to present an overview. It is hoped this paper will contribute to the knowledge of the cui-ui, and that its deficiencies will point out areas where additional research is needed.

HISTORICAL OVERVIEW

Cope (1883) first diagnosed and revised the genus *Chasmistes* and named a new species *C. cujus* from Pyramid Lake. In 1918, Snyder published the first life history information on *C. cujus* and other fishes of the Lahontan System; even at this early date Snyder considered the fate of the cui-ui to be uncertain. Sumner (1940) collected environmental and fishery data from Pyramid Lake and the Truckee River, compiled a chronology of the fishery, and stated that the major cause of the decline of the fishery was the transbasin diversion of Truckee River water.

T. J. Trelease, the first fishery biologist for the Nevada Department of Fish and Game (NFG), did preliminary work on the diet and reproduction of cui-ui (La Rivers 1962). Jonez (1955) and Johnson (1958) (both NFG biologists) worked with cui-ui during the 1950s conducting evaluations of cui-ui behavior and habitat. La Rivers made many observations over the years and developed a life history for cui-ui, incorporating information from previous workers.

Koch (1972, 1973) supplied information on life history, reproductive characteristics, and spawning behavior of cui-ui, Koch and Contreras (1973) advanced artificial hatching techniques, and Koch (1976) summarized available life history information. The U.S. Fish and Wildlife Service operated a cui-ui hatchery in 1974–75. Pyramid Lake Fisheries (PLF) has operated the David L. Koch Cui-ui Hatchery since 1977 and has further refined hatching and rearing techniques.

In 1971 the U.S. Department of the Interior (DI) reported the classification status of the cui-ui. Federal restoration of the species began in 1973 by the U.S. Fish and Wildlife Service (FWS) cui-ui recovery team. This team completed a Draft Cui-ui Recovery Plan in 1977 (Pyle et al. 1977). The 1982 revision of the original Cui-ui Recovery Plan was approved by the FWS and reviewed by DI (U.S. Fish and Wildlife Service 1983).

In 1975 the U.S. Bureau of Indian Affairs (BIA) funded studies on the fisheries of the Truckee River and Pyramid Lake. The results of the Pyramid Lake Ecology Studies, including data on cui-ui ecology, are presented in Sigler and Kennedy (1978). The results of the Truckee River studies are in preliminary FWS reports. McConnell, Galat, and Hamilton-Galat (1978) and Galat and McConnell (1981) discuss Pyramid Lake fish production in relation to potential changes in total dissolved solids (TDS).

In the early 1960s the NFG developed plans for a fishway that would enable upstream migrating fish to bypass the delta and enter the lower Truckee River. The plans were submitted to the Fleischmann Foundation, Reno, Nevada, but the facility was not funded because the Foundation could be given no assurance of a water right. The NFG, along with the FWS and the U.S. Bureau of Reclamation

(BOR), then developed plans for a larger and more elaborate facility. The NFG also lobbied with state and national agencies for the Washoe Project Act, which made funding possible (T. J. Trelease personal communication 1984). The Washoe Project Act was made much more salable by the earlier development, largely by NFG, of highly successful Lahontan cutthroat trout, *Salmo clarki henshawi*, fishery.

In 1975 BOR completed the Marble Bluff Fishway. The FWS operates the Marble Bluff facility and monitors spawning migrations of cui-ui and Lahontan cutthroat trout. Data collected by FWS on cui-ui spawning populations in the lake and fishway are presented by U.S. Fish and Wildlife Service, Nevada Department of Fish and Game, California Department of Fish and Game (1976), Ringo and Sonnevil (1977), and Sonnevil (1977a, 1977b, 1978, 1981). The age structure of cui-ui in 1978 was determined by Robertson (1979). Scoppettone et al. (1981, 1983, and G. Scoppettone personal communication 1983) studied the spawning behavior and habitat requirements of cui-ui in a natural side channel of the lower Truckee River.

Research on the habitat and ecology of fish species in Pyramid Lake was conducted by Vigg (1978a). Vertical distribution patterns and relative abundance are reported (Vigg 1978b, 1980, 1981).

Research on the effects of increasing levels of TDS on cui-ui was initiated by Earl Pyle of FWS during 1975–1978. Chatto (1979) presented preliminary data on hatching success of cui-ui eggs in various proportions of Pyramid Lake water. Lockheed Ocean Sciences Laboratories (LOSL) (1982) studied the effects of various levels of TDS on the embryos, larvae, and juveniles of cui-ui.

T. J. Trelease first reared larvae in 1947, and Kay Johnson and Ivan Young (all NFG personnel) raised them to adult size—about 31 cm. Koch et al. (1979) estimated 91.6% hatching success in controls during nitrogen-species bioassays. However, they were unable to obtain definitive results on toxicity because of high mortality in all treatments and controls. Koch (1981) conducted preliminary temperature tolerance studies of cui-ui embryos and larvae.

Various morphological studies have been conducted on catostomid fishes, including cui-ui. Nelson (1948, 1949, 1961) studied the comparative morphology of the Weberian apparatus, the opercular series, and the swim bladder, respectively. Miller and Evans (1965) studied the external morphology of the catostomid brain and lips. Snyder (1981a, 1981b, 1983) studied larval development of cui-ui, mountain sucker (*Catostomus platyrhynchus*), and Tahoe sucker (*Catostomus tahoensis*) and prepared a key for their identification. Miller and Smith (1967, 1981) discuss the paleohistory, systematics, distribution, evolution, and status of each species of *Chasmistes*.

Donald R. Tuohy, Nevada State Museum, Carson City, has conducted extensive archaeological studies within the Pyramid Lake region; however, the data are largely unpublished. Archaeological finds at Pyramid Lake are reported by Ting (1967) and Tuohy and Clark (1979). Hattori (1982) studied the archaeology of the Winnemucca Lake area and relates the importance of aquatic resources, including cui-ui, to human prehistoric habitation. The importance of the fishery, especially cui-ui, to the native Americans is discussed by Bath (1978). The ethnographic record of Pyramid Lake Northern Paiute fishing is presented by Fowler and Bath (1981). Follett (1963, 1974, 1977, 1980, 1982) has studied cui-ui remains in aboriginal deposits. Stewart (1941) discusses the culture element distributions of the Northern Paiute.

PROCEDURES

Cui-ui were captured with variable mesh bottom-set gill nets in Pyramid Lake and at the Marble Bluff facility on the Truckee River. Vigg (1981) presents a description of fish sampling design and methodology. For age and growth data, fish were weighed to the nearest gram, measured (nearest mm), and sexed internally, except at spawning time. Scales, opercula, otoliths, and fin rays were taken to compare accuracy of aging using different bony parts. The length-weight relationship is expressed by the formula $W = aL^b$ (Sigler 1951), where W = weight (g), L = fork length (cm), and a and b are constants. The value of the constants (a and b) are calculated by the

method of least squares using log transformations of weight and length (log W = log a + log b length). Validity of the aging method was determined by criteria suggested by Van Oosten (1923, 1929, 1944) and Hile (1941). To avoid possible bias, scales and other bony parts were first read without knowledge of the size of the fish. They were read at least three times. The length of body–bony part relationship was calculated according to Tesch (1971). The condition factor $K = Wx10^5/L^3$ was calculated according to Carlander (1969), where W = weight (g) and L = fork length (mm). Age and growth calculations were accomplished using a computer program (Nelson 1976).

Cui-ui eggs and embryos used in this study were obtained from the David L. Koch Fish Hatchery. They were collected at regular intervals postfertilization and preserved in both Bouin's solution and Puckett's fixative. Serial sections of the entire embryo were cut at 8–10 micrometers and stained with hematoxylin and eosin and Mallory's Triple Stain. Embryos to be sectioned were chosen from among the best preserved of 12–15 specimens from each sample. In addition to sectioned material, whole mounts were also used, ranging in age from 9 to 912 hours post-hatching (Bres 1978).

There were 19 water sampling stations located along 4 transects designed to represent the horizontal areas of the lake and to facilitate measuring the influence of the river upon the system. Stations were sampled on a monthly basis from November 1975 through October 1977. Conductivity, oxygen, pH, temperature, and turbidity in relation to time, depth, and location were measured in the field with an InterOcean probe (Model 513D). Measurements were taken at 2-m intervals from the surface to 22 m and at 5-m intervals from 25 m to the bottom. Conductivity measurements were standardized to 25 C. Water samples were collected for analysis of major chemicals and trace elements the third week of every month from January through December 1976 and again in April and September 1977. Samples to be tested for nutrients were collected at least once a month from January 1976 through December 1977. Water samples were collected at the surface (1m), middepth, and bottom levels at the midpoint of each of three transects (Lider 1978). Analyses were done by the Desert Research Institute Water Chemistry Laboratory.

RANGE AND DISTRIBUTION

Four recent species of *Chasmistes* are known: *C. cujus* Cope, *C. liorus* Jordan, *C. brevirostris* Cope, and *C. muriei* Miller and Smith; the latter species, known from a single collection, is now extinct. Two additional extinct species, *C. batrachops* Cope and *C. spatulifer* Miller and Smith, are known only from the fossil record. Miller and Smith (1981) discuss the distribution and evolution of the various forms of *Chasmistes* (Table 1).

Chasmistes is a lacustrine sucker; all living species and most extinct forms are associated with lake systems. However, the oldest known form, *Chasmistes* sp. from the fluvial beds of the Miocene Deer Butte Formation in Oregon, is an exception (Miller and Smith 1981).

The Pyramid Lake cui-ui population is the last remaining pure species of the genus; the other species have considerable hybridization and introgression with *Catostomus* spp. (Miller and Smith 1981). Cui-ui inhabited Lake Lahontan during the late Pleistocene period (Fig. 3). At its maximum extent, approximately 12,000 years BP, Lake Lahontan covered about 22,300 km^2 and received drainage from about 117,000 km^2 (Russell 1885). Fossil cui-ui have been discovered in the Carson Desert, which was once contained in the largest basin of Lake Lahontan; additional *Chasmistes* sp. fossils have been found in the Honey Lake basin to the northwest (Miller and Smith 1981). As Lake Lahontan desiccated during the last 10,000 years, its contiguous basin became nine remnant lakes. Cui-ui persisted for variable lengths of time in these remnant waters until desiccation caused extinction of most populations. Cui-ui was not present in Walker Lake during historical times. This idea is confirmed by the work of Spencer (1977) and Benson (1978a), which indicated Walker Lake was dry sometime during the period 9050 to 6400 years BP.

During historic times cui-ui lived in both Pyramid and Winnemucca lakes and spawned in the Truckee River as far upstream as just below Reno (Snyder 1918). When Derby Dam was completed in 1905, spawning cui-ui

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PCCE (MP)	ICCY (MP)	ICCY (MT)
12.9	18.4	20.1
13.7	19.4	21.1
13.7	14.2	22.3
12.9	15.9	25.7
12.5	15.7	21.1
13.4	19.4	22.3
14.5	19.2	22.5 (est)
13.6	19.7	20.6 (est)
13.1	18.8	22.2
17.0	19.0	22.0
15.6	18.5	20.1
15.9	17.9	20.5
13.6	15.6	20.4
16.3	12.8	21.0
13.5	18.6	
13.6	18.1	
12.8	18.5	
13.3	16.0	
15.5	18.2	
14.3	17.3	
26	34	14

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TABLE 1. The geographic distribution of recent and fossil species of *Chasmistes* (Miller and Smith 1981).

RECENT SPECIES

Common name	*Scientific name*	*Drainage basin*	*Present range*
Cui-ui	*C. cujus* Cope	Lahontan	Pyramid Lake, Nevada
June sucker	*C. liorus* Jordan[A]	Bonneville	Utah Lake, Utah
	C. l.		
	C. l. mictus		
Shortnose sucker	*C. brevirostris* Cope	Klamath River	Upper Klamath Lake, Oregon
Snake River sucker	*C. muriei* Miller and Smith	Snake River	Extinct[B]

FOSSIL SPECIES

Scientific name	*Geologic epoch*	*Geologic formation*	*Paleohabitat*
Chasmistes sp.	Miocene	Deer Butte, OR	Fluvial
C. spatulifer Miller & Smith	Pliocene and Pleistocene-Recent	Glenns Ferry, ID to Adrian, OR	Lake beds
Chasmistes sp.	Pliocene	Glenns Ferry, ID	Lake beds
Chasmistes sp.	Pliocene	Secret Valley, CA	Lake beds
Chasmistes sp.	Pliocene	Honey Lake sediments	Lake Lahontan
Chasmistes sp.	Pliocene	Calcareous sands	Mono Lake
Chasmistes sp.	Pliocene	Teevimom, WY	——
C. batrachops Cope	Pleistocene - Recent	Fort Rock Basin, OR	Fossil lake
Chasmistes cf. *C. batrachops*	Pleistocene - Recent	White Hills, CA	China Lake
C. batrachops	Pleistocene - Recent	Duck Valley, NV	Pleistocene Lake
Chasmistes cf. *C. liorus*	Pleistocene - Recent	Black Rock Canyon, UT	Lake Bonneville
C. cujus	Pleistocene - Recent	Pleistocene gravels, Fallon, NV	Lake Lahontan
C. brevirostris	Pleistocene - Recent	Indian middens, Klamath Lake, OR	Klamath Lake

A. *Catostomus fecundus* = *Chasmistes liorus* × *Catostomus ardens*
B. Based on a single collection from the Snake River below Jackson Lake Dam.

were restricted to the river below that point. As water was diverted to the NRIP via the Truckee Canal, the water level in Winnemucca and Pyramid lakes dropped. Winnemucca Lake dried in 1938. Pyramid Lake and the affluent lower river is the only remaining habitat for cui-ui.

EMBRYOLOGY

Koch (1972, 1976) did limited work on the larval development of cui-ui, finding many similarities to the development of the white sucker, *Catostomus commersoni*, as described by Stewart (1926). Long and Ballard (1976) document the stages of embryonic development of the white sucker and cite diagnostic structural characteristics for each stage. They also review previous work on embryology of other fishes within the order Cypriniformes. Snyder (1983) found that sequences of developmental events are nearly equal for cui-ui, Tahoe sucker, and mountain sucker and typical at least for the tribe Catostomini. However, the latter two species, at any given size, are slightly more developed than cui-ui. The following is a detailed discussion of the embryological development of the cui-ui in a 13 C environment (Bres 1978).

Egg-Embryos

The unfertilized egg of the cui-ui is about 2 mm in diameter and is surrounded by a noncellular chorion. It has one micropyle at the animal pole. After fertilization, during a process known as water hardening, the eggs

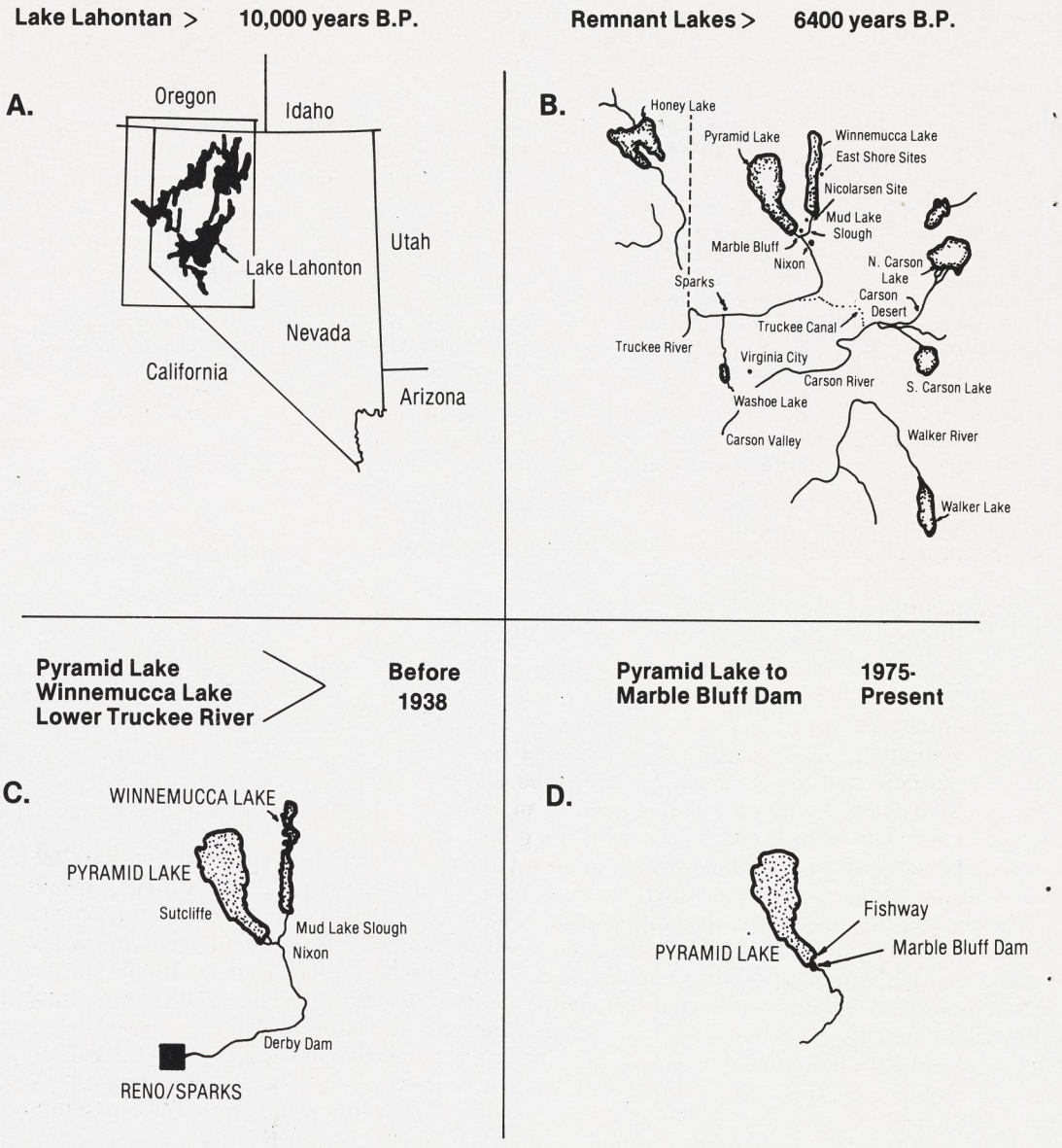

Fig. 3. Decrease in the range of the cui-ui from Lake Lahonton times to the present.

imbibe water and swell to 3 mm. Koch (1976) recorded an 83% increase in egg volume during water hardening, which took 39 minutes. Trelease (personal communication 1984) recorded 75% increase during water hardening and a time of 60 to 75 minutes. The blastodisc appears at 6 hours postfertilization, 0.5 mm in diameter, and is elevated above the surface of the egg at the animal pole. By 18 hours postfertilization, 8 blastomeres are present, with an exponential increase in number thereafter. After 19 hours, "giant" nuclei are seen associated with the syncytial cells of the yolk sac. The marginal periblast is at the periphery of the blastoderm.

At 48 hours postfertilization, the first distinction between the three germ layers is apparent. The neural plate has formed, along with a thickened precursor to the neural tube. The notochord and somites are present.

At 96 to 120 hours, the neural tube and notochord are well developed. Myotomes have differentiated from somites, and the dorsal fin fold has begun to develop. The pronephric ducts are formed anteriorally but are undifferentiated posteriorally. The gut has no lumen and is incomplete posteriorally, and the cloaca has not yet formed.

Anterior neural crest migration occurs at 144 to 168 hours. The diencephalon exhibits cruciform shape. The optic vesicles have developing lenses, and the opticoel joins the diocoel. Auditory vesicles are also present. Myoblasts the length of one somite can be seen. The coelomic cavity is developing between the somatic and splanchnic mesoderm.

At 192 hours cranial ganglia V, VII, and X are visible. Presumptive medulla is developing, and the lateral ventricles are present. The pronephric duct has increased in length, and tubule development is beginning. The liver diverticulum and developing gut are visible. Vitelline circulation is well developed, and the dorsal aorta and postcardinal veins are visible. Precursors of the pigmented retina (a single layer of cells) and the neural retina are forming in the eye. At 13 C hatching occurs at 216 hours.

Larvae

At hatching cui-ui are white and threadlike in appearance, 6 to 7 mm in length, without functional vision, and have only limited powers of locomotion (Table 2 and Fig. 4).

TABLE 2. Time sequence of cui-ui development at 13 C.

AGE (Hours postfertilization)	DEVELOPMENTAL STAGE
0	Unfertilized ovum
6	Formation of blastodisc
18	Eight-cell stage
19	Early blastula
48	Early neurulation, somites present
96 to 120	Neurulation complete, organ development begins
192	Well-developed circulation, appearance of retinal pigment
216	Hatching
(Hours post-hatching)	
9	S-shaped heart
26 to 31	4 pairs of gill arches, optic chiasma forms, secondary reopening of gut begins
51 to 56	6 pairs of gill arches, recanalization progresses to foregut
72	Extensive nerve development, spinal cord differentiated, internal melanophore development
84	Development of lateral line system and external melanophores
120	Begin directional swimming
312	Functional mesonephros, 5 functional gill arches
384	Mouth open, eyes functional, first development of swim bladder
672	Yolk completely absorbed, functional gut
912	Fry actively feeding, approaching adult body form

Central Nervous System.—The anterior curvature of the brain is noted 26 to 36 hours (post-hatch). Considerable nerve development has occurred by 72 hours. The cerebellum is still relatively small compared to the large medulla. The neural tube has differentiated into a spinal cord, and both gray and white matter are present. At 84 hours the potential neurohypophysis of the pituitary is developing in the brain. The III and IV ventricles are present, with the Aqueduct of Sylvius connecting them; the region of the epiphysis is also beginning to develop. Spinal ganglia

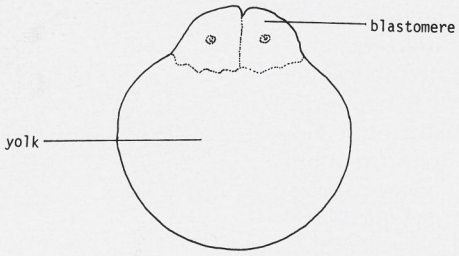

Fig. 4a. 6 hours postfertilization

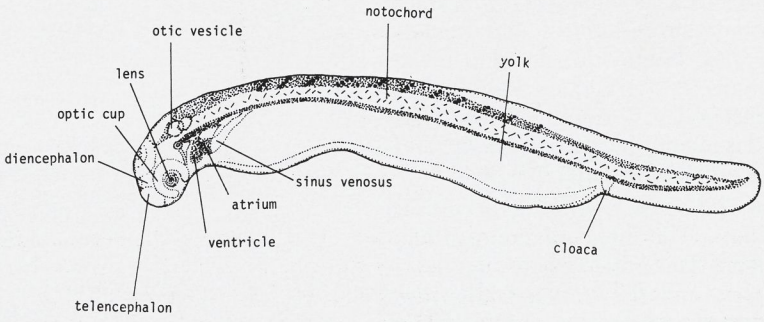

Fig. 4b. 9 hours post-hatching

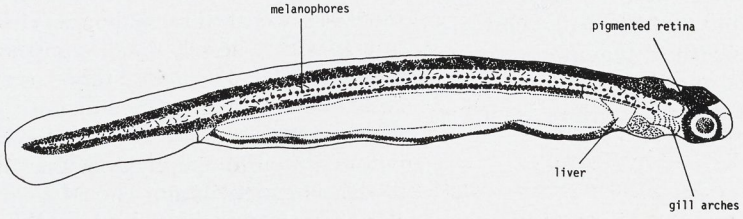

Fig. 4c. 4.5 days post-hatching

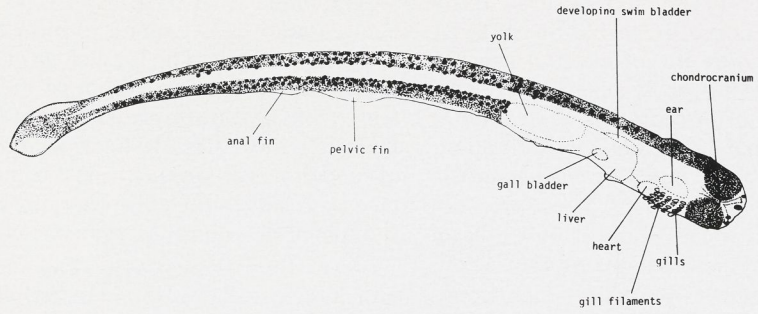

Fig. 4d. 21 days post-hatching

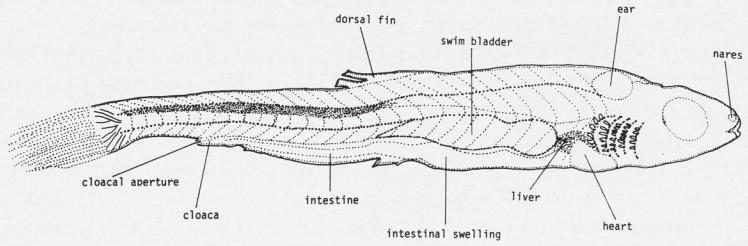

Fig. 4e. 38 days post-hatching

Fig. 4. Embryonic stages of development of the cui-ui.

are visible along the spinal cord. At 384 hours the epiphysis continues to develop. The pituitary and hypothalamus are visible, although no differentiation has occurred in the pituitary. Motor neurons are well developed in the mesencephalon. At 504 hours the developing chondrocranium is visible.

Eye.—The optic cup and retina continue to develop after hatching occurs. The optic chiasma is first observed at 26 to 31 hours (post-hatch), with the optic nerve connected to the retina. The horseshoe-shaped retina, derived from the optic cup, is apparent at 51 to 56 hours. At this time the oculomotor nerve is visible, extending from the brain to the eye region. By 72 hours the lens is present and the pigmented retina is represented by a thin layer; however, no differentiation has occurred in the sensory portion of the retina. Presumptive cornea has formed by 84 hours, and differentiation in layers of sensory retina has occurred. The optic nerve is attached to the retina. Extrinsic ocular muscles are well developed. By 120 hours, heavy pigmentation has been laid down on the retina. After 384 hours the pigmented iris, cornea, lens, and many sensory layers of the retina are visible. The eyes are functional and capable of movement.

Ear and Lateral Line.— Seventy-two hours post-hatching, the otic vesicle, the rudiment of the inner ear, begins to develop. The first complete distinction between the dorsal sacculus and the central utriculus takes place in the otic vesicle at 84 hours post-hatching. At this time the first indication of lateral line system development occurs. By 168 hours the otic vesicle is well developed. After 384 hours of larval development, the otic capsule has divided into 3 parts, the latter part being completely closed off. Otoliths are visible in the inner ear, and the cranial nerves that supply the ear are visible. The vestibular ganglia has developed outside the otic capsule from the stato-acoustic nerve (VIII).

Olfactory Sense and Taste Buds.—By 20 hours the olfactory placodes are well developed in the anterior portion of the head. The

neural connection of the nasal placode to the brain (olfactory nerve) is visible by 26 to 31 hours. By 168 hours the olfactory organ has developed from the nasal placode. By 384 hours indentations are forming at the site of the future external nares. The mouth is open, and developing taste buds are visible in the mouth and gills by 384 hours. These are very abundant on the head, mouth, and gills of adults and compensate for incomplete development of the internal nares.

Gills.—Four pairs of gill arches are visible at 26 to 31 hours. The aortic arches leave the center of the gill arch to fuse together and open into the conus arterious. At 51 to 56 hours six pairs of gill arches are present and the gill cleft is developing. By 60 hours each of the six pairs of well-developed gill arches has a central core, the aortic arch. By 72 hours the aortic arch has increased substantially in size. At 84 hours the first gill cleft has opened. By 312 hours the 6 primitive gill arches have been reduced to 5 functional gill arches, the definitive adult condition. Each arch has at least 3 filaments composed of loops of capillaries. After 384 hours of development, gill filaments are evident, as are gill cartilages associated with muscles for moving the gills.

Heart.—The S-shaped heart is visible 9 hours post-hatching. After 20 hours the endocardial cushion, which is the precursor to valve development, is forming in the atrio-ventricular canal. Separation between endocardium and myocardium is pronounced by 56 hours post-hatching. The heart and associated vessels are well developed by 72 hours. Cardiac jelly is visible after 82 hours. After 120 hours all 4 chambers of the heart and the atrio-ventricular canal are visible. After 312 hours the muscular wall of the heart is well developed and the ventricle has become trabeculated. By 384 hours all blood vessels contain eosinophilic plasma.

Muscle.—Myotomes and myocommata are well developed by 9 hours. By 26 to 31 hours connective tissue is present in the myocommata. At 72 hours myofibrils appear as ribbons around the periphery of the muscle cells; this conforms to the standard configuration of the adult fish.

Skeleton.—After 20 hours the sites of the future chondrification of the ribs are visible as individual swellings along the dorso-lateral intersegmental myosepta. By 51 to 56 hours condensation is beginning to form the initial skeletal elements. The trabeculae of the chondocranium are visible, although they are not true cartilage but simply condensations of the mesenchyme. After 312 hours a large number of caudal rays are present. At 384 hours cartilage is present in the gill arches, opercula, and the roof of the mouth (precursor to palate).

Liver and Pancreas.—The liver primordium is well developed by 20 hours. At 26 to 31 hours the sinus venosus has been displaced to a crescent shape at the side of the liver. The liver primordium is well developed by 84 hours; a pancreatic rudiment is visible next to the intestinal swelling. The liver has an adult pattern of organization and is functional by 384 hours. The pancreas is forming lobules that will later spread out forming the adult diffuse pancreas. The gall bladder is visible; bile and pancreatic ducts are separate and fuse together at the entrance to the gut.

Kidney.—At 9 hours the pronephric ducts join with the intestine posteriorally to form the cloaca. By 26 to 31 hours, ciliated nephrostomes, the opening of the kidney tubule to the coelom, have developed in the pronephros, and coelomic fluid is pumped into the tubule. After 72 hours of larval development, kidney tubules are well developed in the pronephros. For the first time, the mesonephros and mesonephric tubules are visible. At 84 hours the mesonephric duct is visible, opening into the mesonephros and contacting the cloaca. By 312 hours the mesonephros has greatly enlarged, is very well developed, and has reached a functional state. At 672 hours the mesonephric duct and anus empty together into the cloacal aperture.

Alimentary Canal.—The pronephric ducts join with the intestine posteriorly to form the cloaca 9 hours post-hatching. The tiny, solid gut begins to form the loop of the intestinal swelling at about 20 hours. The larval cui-ui, like the adults, do not have a true stomach since it contains no glands. At 26 to 31 hours the secondary reopening of the gut begins, small in the liver mass but enlarging in the midgut region posterior to the liver. Mesenteries supporting the gut are visible. Absorptive cells are apparent in the yolk sac, and the mouth cleft is present. Further recanalization of the foregut is occurring at 51 to 56 hours. At

72 hours there are many secondary openings in the foregut. Also the lumen of the gut has greatly increased from 1 to 2 to 10 to 15 micrometers in diameter. At 84 hours the loops of the gut are beginning to form; early differentiation of the intestinal swelling and visceral cavity occurs. The pharyngeal cavity is open at 120 hours. After 384 hours the mouth is open, and many mucous-secreting cells are visible in the oral cavity. Material present in the pharynx suggests feeding, although some parts of the pharynx are still undifferentiated. The gut is broadly open and has developing longitudinal folds. From 384 to 504 hours the yolk sac is greatly diminishing in size. After 672 hours of larval development, the yolk is absent and the gut is functional, with food present in the intestine. By 840 hours the larvae are 20 to 25 mm long (Koch 1976). After 912 hours fry are actively feeding and the digestive tract is filled with food.

Integument and Pigmentation.—By 20 hours lateral fin folds are well developed, and many mucous secreting cells are visible in the ectoderm. Connective tissue is present in the dermis of the skin at 26 to 31 hours. After 72 hours the epithelium is still simple, and many secretory cells are present. Melanophore development is beginning internally. At 84 hours goblet cells are observed in the epithelium. Granular cells, filled with eosinophilic granules, are present, characteristic of the adult condition. Both small and large external melanophores are visible by 120 hours posthatching. At 384 hours mucous-secreting goblet cells are present in the skin.

Swimming.—After 18 hours the larvae are 8 to 9 mm long, and sudden bursts of energy constitute their initial swimming attempts; at 192 to 240 hours the larvae are 12 to 14 mm in length and continually swim at the surface (Koch 1976). Between 240 to 360 hours they swim to keep their position in the water column (Koch 1976). After 384 hours the pneumatic duct enters the gut from the developing swim bladder, and at 504 hours the swim bladder is clearly visible. The swim bladder has increased in size during 672 hours.

Identification.—Larval and juvenile cui-ui are sometimes difficult to identify in Pyramid Lake; they are easily confused with another resident catostomid, the Tahoe sucker. This may, in part, account for the fact that relatively few cui-ui less than 300 mm in length have been identified. Ramsey (letter to E. A. Pyle, 16 September, 1974) offers the following points of contrast between the two larvae:

Ventral-Pigmentation: A consistent character for distinguishing larval stages of Tahoe sucker from larval cui-ui is the presence of a superficial row of melanophores on the midventral skin posterior to the pectoral basis. This abdominal pigmentation is generally absent in cui-ui, although a row of melanophores sometimes is present but confined to the breast anterior to the pectoral bases. The row of midventral melanophores in larval Tahoe suckers is still present at age 66 days (17 to 19 mm total length).

Intestinal Coiling: At age 66 days the intestine of the Tahoe sucker loops far anterior in contrast to the cui-ui, where it is either straight or has a left twist.

Mouth: The lips of the Tahoe sucker are thicker and the mouth is placed further ventrally than in the cui-ui.

Other: A character sometimes useful at ages earlier than 66 days is the presence in cui-ui of a depigmented "one to one" on top of the head, just posterior to the eyes. There is considerable occluding of this pigmentation by age 66 days.

Snyder (1981a, 1981b, 1983) studying larval development of cui-ui in comparison to the other catostomids that spawn in the Truckee River system, i.e., Tahoe sucker and mountain sucker, developed a taxonomic key that separates the larvae and early juveniles of the three species. Snyder concludes the larvae can be separated on the basis of midventral pigmentation, peritoneal pigmentation, gut-loop formation, and mouth characters.

The following differential characteristics are included to complement previous descriptions of larval development and morphology (Snyder 1983). At a total length (TL) of 11 to 21 mm, cui-ui are characterized by absence of midventral melanophores on the head or abdomen anterior to the bases of pelvic fin or their precursors and anterior to the vent. If midventral melanophores exist, they are present as a short line only in the branchial and heart regions between and anterior to pectoral fin bases. Mesolarvae have a straight gut until about 19 mm TL; metalarvae to 21 mm may develop a primary loop extending forward less than two-thirds of the length of the stomach and not crossing over the stomach. Metalarvae have peritoneal pigmentation largely restricted to the dorsal and dorsalateral visceral cavity.

The following characteristics apply to metalarvae > 21 mm and juveniles < 50 mm. The pigmentation of the peritoneum is mostly lim-

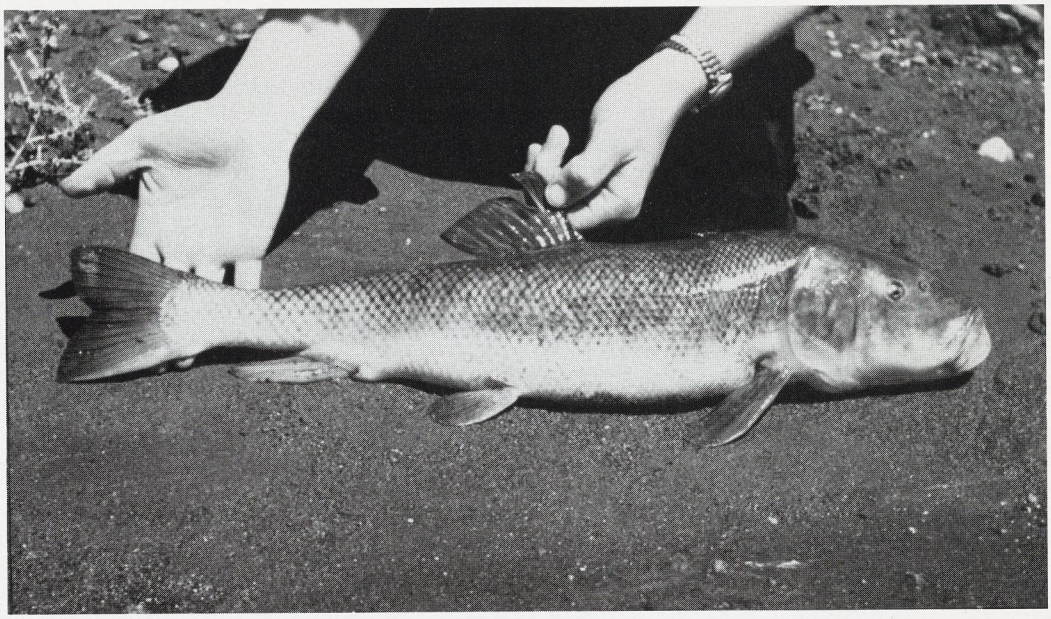

Fig. 5. Adult female cui-ui. Photo by Thomas J. Trelease.

ited to the dorsal and dorsalateral visceral cavity. The primary loop of the gut is relatively straight along the left side of the stomach until about 30 mm TL, at which size secondary loops cross the stomach in an S-shape, persisting through 50 mm TL. The mouth is terminal—usually slightly oblique but sometimes very low and almost horizontal, approaching a subterminal condition.

ADULT MORPHOLOGY

Description

The cui-ui is a large, big-mouthed sucker. The head is wide and somewhat round in cross-section. Its interorbital space is greater than half the length of the head. The mouth is unsuckerlike with a ventro-terminal position. The lips are thin and obscurely papillose. The lower lip is somewhat pendant and divided by a wide median notch. The cui-ui is coarsely scaled, with counts of 13 to 14 above the lateral line, 59 to 66 along the lateral series and 22 to 26 around the caudal peduncle. The total body length is 9 times that of the dorsal fin base. The length of the anal fin, from the insertion to the tip, is about one sixth the total body length. Fin ray counts are: dorsal, 10 to 12; anal, 7; and caudal, 8 or less. The caudal is weak to moderately forked. The caudal peduncle is thick, with the smallest depth going 12 times into standard body length (SL). In triangular section, the pharyngeal teeth are delicate. The last pharyngeal arch bears a row of more than 10 comblike teeth confined to a single row. The swim bladder is 2–celled; the peritoneum is nearly black. Each gill raker is branched like broccoli (Fig. 5).

Sexual Dimorphism

Breeding males display a brilliant red to brassy color on the sides; in general they are black or brown above, fading into flat white below. Females have a bluish gray cast year-round. Female cui-ui attain greater length and heavier weight than males. During the spawning season the vent of females becomes swollen and extended, whereas males develop nuptial tubercles on their fins. Apparent sexual dimorphism exists in the meristics associated with fin size (Table 3). The length of the base of the dorsal and anal fins, the height of the dorsal and anal fins, and the length of the pectoral, pelvic, and caudal fins are all proportionally greater for males. Snyder (1918) refers to differences between the sexes:

> The females are more stocky than the males, and with their huge heads, large rounded bodies, and relatively

TABLE 3. Meristics of *Chasmistes cujus* from near the mouth of the Truckee River (Snyder 1918).

Morphological characteristic	Mean measurement Males n=11	Females n=7
Standard length (mm) ***	427.1	487.3
range	(410–444)	(445–538)
Percent of body length		
Length head	28.0	27.8
Depth body *	21.1	22.4
Depth caudal peduncle	8.5	8.2
Length caudal peduncle	15.8	15.2
Length snout	12.9	13.2
Diameter eye	3.1	2.9
Interorbital width	12.4	12.5
Depth head	18.7	18.6
Snout to occiput	22.3	22.0
Snout to dorsal	51.3	50.5
Snout to ventral	58.1	58.4
Length base of dorsal ***	15.1	13.3
Length base of anal ***	9.4	8.1
Height dorsal	12.9	12.5
Height anal ***	19.9	15.6
Length pectoral **	18.9	17.5
Length pelvic ***	13.8	11.6
Length caudal ***	20.4	18.4
Dorsal rays	11.1	10.7
Anal rays	7.2	7.0
Scales lateral line	62.1	61.6
Scales above lateral line	13.6	13.9
Scales below lateral line	10.4	10.1
Scales before dorsal	31.6	30.3

* Significant differences between sexes, $P<0.05$.
** $P<.01$
*** $P<.001$

short fins are very ungainly looking fish. The scales and fins are without tubercles.

Snyder (1918) describes the differential coloration patterns between the sexes. He also reports that Indians could differentiate cui-ui from Pyramid and Winnemucca lakes by the grayer color of the Winnemucca cui-ui, although he was unable to detect any difference.

Comparative Morphology

The ventro-terminal position of the mouth is a diagnostic characteristic of *Chasmistes* spp. It is so exceptional among the usually ventral-mouthed sucker family that it has been regarded as an extreme specialization; however, certain primitive suckers (e.g., *Amyzon* and *Ictiobus cyprinellus*) and presumed sucker ancestors are also characterized by relatively terminal mouths (Miller and Smith 1981). Cui-ui is the largest living species of *Chasmistes*. Snyder (1918) collected specimens ranging from 410 to 670 mm in SL.

Of various adult meristic data summarized from the literature, Snyder (1983) determined that lateral series scale counts prove to be diagnostic in separating cui-ui (59 to 66) from mountain sucker (75 to 100) and Tahoe sucker (79 to 95). For juveniles, Snyder found this character useful only when squamation is complete, usually by 35 to 50 mm TL.

The comparative morphology of Catostomidae has been studied with reference to the swim bladder (Nelson 1961), the opercular series (Nelson 1949), the Weberian apparatus (Nelson 1948), and the brain and lips (Miller and Evans 1965). *Chasmistes* spp. have a two-chambered swim bladder that is characteristic of all catostomids except *Moxostoma*, which has a three-chambered structure. It is the posterior chamber in catostomids that regulates buoyancy. The usual catostomid swim bladder is 35 to 45% of the SL of the fish (7% by volume); however, the cui-ui swim bladder is only 32.1% of SL (Nelson 1961).

Nelson (1949) presents a generalized composite of the catostomid opercular series, which consists of a large operculum, relatively small suboperculum and interoperculum, and invariably three branchiostegal rays. On the basis of the opercular series, the genera of Catostomidae can be arranged into three well-defined groups; *Chasmistes* belongs to the group including *Catostomus* and *Xyrauchen* (Nelson 1949).

The Weberian apparatus of catostomids includes the first four vertebrae and associated structures that form two separate functional units. *Chasmistes* has the same general morphological pattern as *Catostomus* and *Xyrauchen*; however, it differs in having enlarged esophageal supports and obliterated second to third intervertebral space (Nelson 1948). Based on the comparative morphology of the Weberian apparatus, Nelson concludes *Chasmistes* is an early divergent of the catostomid stock.

Miller and Evans (1965), studying the morphology of the brain and lips in catostomids, conclude:

> Their principal value probably lies in providing a basis for making inferences about the life history, and especially the habitat preferences and feeding behavior of little-known species.

Thus, morphological evidence may shed light on aspects of the ecology of cui-ui about which there has been much speculation. The

facial lobe of the brain is associated with taste buds on the lips and skin, whereas the vagal lobes receive fibers from taste buds in the mouth and pharynx. The brain morphology of cui-ui is unique in several ways: the optic lobes are small and separated, the postcerebellar medulla is elongated, and the vagal lobes are well developed but located more posteriorly than is usual in catostomids. The overall pattern suggests a well-developed "mouth tasting" apparatus (Miller and Evans 1965). Suckers that have large vagal lobes are characteristic of lotic habitats, and mouth tasters probably sort food within the oral cavity. Thus the cui-ui is probably not a sight-feeder in surface waters but may use the oral cavity to sort out food (e.g., algae and invertebrates). Other genera with well-developed vagal lobes include *Xyrauchen*, *Ictiobus*, and *Carpiodes*.

AGE AND GROWTH

The cui-ui is a slow-growing, long-lived fish, living 18 or more years (Robertson 1979). Scoppettone (report to Desert Fishes Council 1983) stated it may live much longer ($\geq$ 40). Growth in length is rapid for the first 4 to 5 years and slower thereafter. Annuli in older fish are formed between June and August; in younger fish it may occur the first week of June.

Back-calculated fork length (FL) at scale formation is 46.0 mm for known age fish (I to III), from the NFG Washoe Rearing Station, Reno. The calculated FL was skewed substantially higher when advanced age groups (IV and VI) from Pyramid Lake were added. In aquarium-reared fish, E. Pyle (personal communication 1977) found they started forming scales at 49.0 mm FL, and fish 50 mm had from 3 to 7 scales at the base of the caudal peduncle.

Scales are judged not to be reliable for aging cui-ui older than age VI. Other bony parts, otolith, opercula, and fin ray, are more nearly reliable. No technique is reliable when there is no, or almost no, growth and no discernible annulus. This is a definite possibility in older cui-ui. There is reasonably good agreement between fin rays and otoliths and excellent agreement between otoliths and operculum through age XIII (Table 4). There was generally good agreement for otolith, opercula, and scale in age I to IV. Data from opercula were chosen because it is reliable and easy to collect and process. Since growth differences were not significant, sexes are combined (Table 5). The absolute growth is in good agreement with calculated growth (Fig. 6). The body fork length-opercula (X) relationship, sexes combined, is: $FL = 229.2 + 7.0 \times (r^2 = 0.92)$.

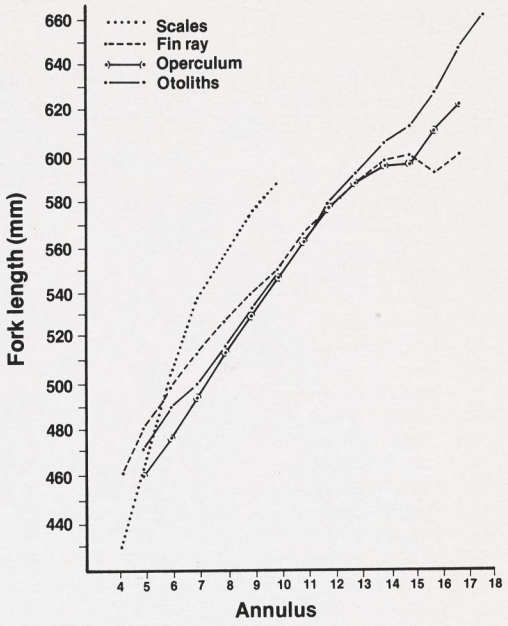

Fig. 6. Absolute growth rates using four methods of age assignment (scales, fin rays, operculum, and otoliths) for cui-ui collected from Pyramid Lake, Nevada, 1978 (Robertson 1979).

The body length–bony part radius regressions are highly correlated: fin ray ($r^2 = 0.93$), opercula ($r^2 = 0.92$), otolith ($r^2 = 0.80$), and scales ($r^2 = 0.63$) (Robertson 1979).

The drop in numbers of fish older than age XV may be attributed largely to natural mortality or no growth, but the low numbers of fish in some of the younger age groups are, in part, a result of moderate to weak year classes (Table 6). Sonnevil (1978) suggests reduced spawning populations and consequent weak year classes can be attributed to reduced river flows at the time cui-ui spawn.

There appears to be good correlation between strength of year classes and flow levels of the river for 5 of the 12 years and poor correlation for 3 of the 12 years (Table 7).

TABLE 4. Comparison of assigned age by various aging methods for 28 cui-ui, sexes combined. Collected April to July 1978 from Pyramid Lake, Nevada.

		Methods of age assignment				
ID#	Fork length (mm) at capture	Scale age	Fin ray age	Operculum age	Otolith age	Centrum age
32A	599	8	10	11	10	—
33A	587	8	11	11	11	—
36A	612	8	12	13	13	—
17A	638	8	13	13	14	—
14B	584	8	—	11	11	—
16B	615	8	11	11	11	—
YY–3	565	8	11	—	12	—
24A	604	8	11	11	11	—
17	578	8	12	12	12	—
24	633	8	15	14	15	—
31	607	8	11	12	12	—
33	618	8	11	12	12	—
9B	588	8	—	11	11	—
20A	618	8	—	14	13	—
21A	615	8	—	12	12	—
28A	591	8	12	12	12	—
8B	588	8	7	12	12	—
4B	620	8	—	13	13	—
27A	648	9	14	14	14	—
38A	632	9	12	13	13	—
19A	609	9	—	11	12	—
AA	610	9	—	12	12	—
F	573	9	—	10	11	10
E	638	9	—	16	16	—
2B	598	—	—	10	10	—
ZZ-B	575	—	—	11	—	—
3B	601	—	—	12	12	—
23	632	—	13	13	13	—

TABLE 5. Calculated average fork length and annual growth increments using opercula of 79 cui-ui, sexes combined. Collected April 1978 to July 1978 from Pyramid Lake, Nevada (Robertson 1979).

Age	Number of	Mean calculated fish length (FL-mm) at each annulus												
group	fish	5	6	7	8	9	10	11	12	13	14	15	16	17
V	13	466												
VI	12	465	490											
VII	3	453	481	499										
X	6	451	470	485	511	527	468							
XI	10	455	477	499	518	539	559	576						
XII	17	453	471	494	512	530	547	563	583					
XIII	10	447	468	492	511	523	546	562	579	596				
XIV	4	455	478	493	515	531	547	566	580	594	611			
XV	1	453	474	495	508	522	529	536	553	564	578	599		
XVI	1	418	440	460	484	508	522	543	564	578	585	599	613	
XVII	2	440	457	471	488	507	524	540	550	564	583	596	610	624
Total number		79	66	54	51	51	51	45	35	18	8	4	3	2
Grand average (mm) calculated fork length		459	475	493	512	530	548	564	578	589	597	598	611	624
Range (mm) in calculated length		418–488	439–529	467–536	484–533	484–571	495–592	515–606	522–634	536–634	553–620	564–627	578–641	592–655
Length increments (mm)		459	16	18	19	18	18	16	14	11	8	1	13	13

TABLE 6. Age and year class composition of 665 cui-ui sampled in Pyramid Lake, Nevada, 1978 (Robertson 1979).

Age class	Year class	% Composition	Number of fish
IV	1974	6.0	37
V	1973	32.0	211
VI	1972	22.0	149
VII	1971	7.0	49
VIII	1970	5.0	34
IX	1969	3.0	18
X	1968	2.0	16
XI	1967	2.0	14
XII	1966	4.0	27
XIII	1965	4.0	28
XIV	1964	3.0	21
XV	1963	6.0	41
XVI	1962	2.0	13
XVII	1961	0.9	6
XVIII	1960	0.2	1

There appears to be good correlation between strength of year classes and flow levels of the river for 5 of the 12 years and poor correlation for 3 of the 12 years (Table 7).

Robertson (1979) determined the length-weight relationship for 139 females, ranging from 453 to 653 mm FL, and for 147 males, ranging from 448 to 577 mm FL. Only spawned fish were included in these data. The relationships for males and females are: males $\log_{10} W = 3.4725 + 2.4639 (\log_{10} L)$ ($r^2 = 0.77$); females $\log_{10} W = 4.5046 + 2.8485 (\log_{10} L)$ ($r^2 = 0.93$). Males weighed less than females of equivalent length and age. This is in agreement with Johnson (1958) and Koch (1972). The length-weight relationship in the 1975 to 1977 Pyramid Lake study (Robertson and Koch 1978) was: $\log_{10} W = -1.240 + 2.5738 (\log_{10} L)$; this is in agreement with work done by Robertson (1979) in 1978–1979.

The condition factor, or general robustness of the fish, K(FL) for spent (spawned out) fish ranged between 1.08 and 1.64, with a mean of 1.21 for females and 0.81 to 1.61 and a mean of 1.20 for males (Robertson 1979). The condition factor decreases moderately with an increase in length, and the decrease is higher for males than females. Condition factors for the 1976 to 1977 study showed similar trends (Table 8).

TABLE 7. Discharge in cubic feet per second (cfs), of the Truckee River near Nixon, Nevada, for the calendar years 1962–1973 (USGS 1962–1973) and year class–levels of flow relationship.

Year	Age group	Mean flows (cfs) by month				Strength of year class*	Level of river flows*
		April	May	June	July		
1962	XVI	315.0	229.0	31.3	18.8	1	3
1963	XV	183.0	1391.0	926.0	53.7	1	2
1964	XIV	53.4	93.2	48.3	26.2	3	3
1965	XIII	580.0	1325.0	515.0	62.2	2	1
1966	XII	64.6	61.4	47.0	33.2	2	1
1967	XI	5.9	7.5	11.4	31.7	3	3
1968	X	321.0	67.9	52.4	38.8	3	3
1969	IX	3392.0	3454.0	3469.0	430.0	3	1
1970	VIII	530.0	212.0	291.0	445.0	2	2
1971	VII	770.0	1234.0	1744.0	451.0	2	1
1972	VI	236.0	249.0	110.0	43.3	1	3
1973	V	854.0	991.0	453.0	321.0	1	1

*Rated on a 1 to 3 scale, where 1 is strong and 3 is weak.

Although 1969 was a high water year, a weak year class resulted. According to Robertson (1979), this appears to contradict the hypothesis of high flows and successful cui-ui spawning; however, it is pointed out this was the year of exceptionally high suspended sediment discharges, which may have been lethal to fertilized eggs.

Koch (1972) reports the mean age of spawning cui-ui in 1971 and 1972 as 7.5 and 7 years, respectively. These represent the strong year classes produced in high water years of 1963 and 1965. Koch also found a low number of fish representing ages IV, V, and VI in 1971 and 1972.

FOOD AND FEEDING

The diet of cui-ui is not well known; however, we made some observations under artificial conditions. Koch (1972, 1976) reports larval cui-ui, older than 20 days, readily consume zooplankton introduced into an aquar-

TABLE 8. Length, weight, and condition factors $K = W \times \frac{10^5}{FL^3}$ for cui-ui, sexes combined, Pyramid Lake, Nevada, 1976 to 1977 (Robertson and Koch 1978).

Fork length (mm)	Weight (g)	K factor
378	566	1.04
401	659	1.02
424	761	0.99
447	872	0.97
472	1002	0.95
495	1133	0.93
518	1273	0.91
544	1444	0.89
589	1771	0.86

Fig. 7. An adult copepod, *Diaptomus sicilis*, a common food of cui-ui.

ium of lake water. He reports the zooplankter *Moina hutchinsoni* is most preferred by larvae, presumably because it has limited mobility, whereas *Diaptomus sicilis* is the least preferred zooplankter (Fig. 7). We have observed aquaria-reared larvae and juvenile cui-ui grazing on periphyton growing on rocks. Since zooplankton is not abundant in the river habitat of larval cui-ui, periphyton is probably important in their diet. When young cui-ui first enter the lake, they may feed both on periphyton and zooplankton. In the David L. Koch Hatchery larval and juvenile cui-ui feed on algae on the sides of the tanks, as well as on commercial fish feed (A. Ruger personal communication 1983).

Snyder (1918) found spawning adults do not feed; he states: "The stomachs of all specimens examined were devoid of food." Koch (1972) reports cui-ui examined during spawning migrations of 1971 and 1972 had not recently fed. Examination of fish during the spawning migration at the Marble Bluff facility also confirm these observations.

Johnson (1958) reports that, of 46 adult cui-ui examined, 43 had eaten zooplankton (93.5% occurrence), 4 sand and mud (8.7% occurrence), 2 unidentified material (4.3% occurrence), and 1 insects (2.1% occurrence). La Rivers (1962) reports T. J. Trelease examined specimens taken in commercial net hauls and found a mixture of algal filaments with zooplankton fragments. From this information La Rivers (1962) concludes, "It seems probable that most of the feeding is done about rocks where thick algae coatings are heavily populated with micro-crustacea." Based on the cui-ui's fine and numerous gill rakers, La Rivers hypothesized, "The strong possibility exists that they can extract useable quantities of micro-crustacea from the open lake waters." T. J. Trelease (personal communication 1984) observed cui-ui in large doughnut-shaped schools near the surface over deep water and far from shore first in 1954. He assumed they were feeding since tui chub form similarly shaped schools when they are feeding. He saw these schools somewhat frequently as late as 1968. Vigg (1978a, 1980) documented that adult cui-ui primarily inhabit the shallow benthic areas and not the limnetic water column. It may be that when they inhabit the benthic zone they generally feed further off the bottom than species of suckers with ventral mouths.

REPRODUCTION

Migration

Snyder (1918) and Scoppettone et al. (1981, 1983) made detailed observations on cui-ui spawning migrations. Snyder observed the annual cui-ui spawning run begins about April 15, depending on the condition of the river. La Rivers (1962) states it is about a month later than in Snyder's time as a result of river conditions: it extends from mid-May to early June. However, Trelease (1971) reports cui-ui may spawn as early as April and as late as July, when a surge of fresh water often triggers the spawning run. The cui-ui apparently homes fresh water, including springs. Scoppettone et al. (1981) also found a sudden heavy surge of very turbulent water often triggered spawning activities, even in the daytime. The cui-ui prefers depths of water for spawning that

range from 9 to 43 cm, velocities that range from 23 to 87 cm/sec, and substrate with about 60% gravel.

Historically, cui-ui spawning runs up the Truckee River only occasionally reached downtown Reno, a distance of over 100 km (Snyder 1918). Today they generally run no farther upstream than 15 to 20 km, although they can go further. Koch and Contreras (1972) report spawn-laden cui-ui reach exhaustion in 18, 10, 2, and 0.5 hours at velocities of 1.2, 1.8, 4.6 and 5.2 m/s, respectively.

Spawning Behavior

Spawning cui-ui often choose the head of gravel bars, where the flow is rapid and the substrate relatively free of silt (McGarvey 1974). At times the dorsal fins of the cui-ui project above the water, and in very shallow places, where there is much crowding, the entire backs of the fish are exposed (La Rivers 1962). Trelease (1971) notes the numbers of cui-ui at the mouth of the Truckee River in past years were so immense at spawning time that fish near the surface were literally forced out of the water, and during periods of peak activity schools of fish covering 0.4 ha or more would form a mass of writhing fish on the surface of the water. Some runs of cui-ui were so extensive that, as fish worked their way upstream in dense schools, their numbers actually blocked the flow of water and diverted it around them. As a result, a new channel was sometimes cut through the sandy delta, leaving large numbers of fish stranded.

Migrating and spawning cui-ui are more active at night than in daytime (Snyder 1918). Scoppettone et al. (1983) found that peak spawning occurs between the hours 2000 and 0600 over a 3–day period and postulate that nocturnal spawning lessens egg predation. Adhesive eggs are broadcast over a large area (Koch 1973). One spawning act, lasting from 3 to 6 seconds, is participated in by 1, or occasionally 2, females and from 2 to 4 males; although a typical spawning act has 1 female and 2 males. Scoppettone et al. (1983) found the most active male spawned 294 times, the most active female 114 times. The length of the spawning run for individual males was 3 to 5 days, for females 2.5 to 4 days.

Just prior to spawning, two males position themselves on either side of a female, the heads of the males just aft of the female's head. With bodies touching and quivering, the female deposits eggs, followed by the males expelling sperm. The cupping and vibration of the male's caudal, along with the female's caudal, creates an eddy preventing the eggs from drifting away before they are fertilized (Scoppettone et al. 1983). Although the cui-ui does not build a nest, the fanning of the caudal fins serves to clear the area of silt.

Optimum Hatching Temperature

In an 8–day period when temperatures ranged from 13.8 to 20.8 C, with a mean of 16.7 C, mean viability of the embryos was 47% (Scoppettone et al. 1981). Koch (1981) found 13.9 C optimum for cui-ui egg incubation; embryos incubated at 17.8 C had a 60% survival to hatching, whereas embryos incubated at 21.7 C had a 30% survival. High temperatures cause preemergence of larva, and a lower rate of survival (Lockheed Ocean Sciences Laboratories 1982).

Larval Migration

Larval peak downstream migration is 14 or more days after hatching (Scoppettone et al. 1983). Hatchery-reared larval cui-ui, 15 to 18 days old, released in 3 areas of the Truckee River, began migrating downstream immediately. The peak migration occurred the night of release followed by several days' lull. All three groups showed a tendency for immediate outmigration (Scoppettone et al. 1981). It should be noted that our embryological studies show that larvae are not developed well enough to feed or swim actively before 21 to 18 days at 13.6 C. It may be that early migrations (< 28 days) greatly reduce chances of survival.

Lake Spawning

There are several reports of cui-ui spawning in the freshwater–lake saline interface. Snyder (1918) reports, "On May 1, 1913 large numbers of cui-ui were found depositing eggs along the shallows near some springs on the southwest shore." Johnson (1958) observed ready-to-spawn cui-ui around the periphery of the lake. Koch (1973) documented the spawning behavior of cui-ui near the inflow of freshwater springs (0.014 cms) in 17.3 C lake

TABLE 9. Number of cui-ui eggs taken at the Marble Bluff facility, 1978–1983 (Source: Alan Ruger, Pyramid Lake Fisheries director).

	Number of spawners		Number of eggs	Eggs per female
	Male	Female		
1978	188	226	4,838,660	21,410
1979	112	92	2,706,308	29,416
1980	333	320	12,140,480	37,939
1981	166	158	5,437,886	34,417
1982	422	436	17,707,268	40,613
1983	184	244	13,706,700	56,175
Totals and weighted average	1,405	1,476	56,537,197	38,304

water in the Hell's Kitchen area, which is approximately 29.5 km north of the Truckee River. Most biologists agree that cui-ui spawn in the lake (> 5000 mg/l TDS) as well as in the river (< 600 mg/l TDS), but the success of the lake spawning is not known. Observed lake spawning has been in the vicinity of fresh water, e.g., springs or stream-lake interfaces (Koch 1973). T. J. Trelease (personal communication 1984) lists seven places around the lake where he observed cui-ui spawning over the years. Experiments by LOSL (1982) and Chatto (1979) indicate that eggs must be water hardened in fresh water (< 600 mg/l TDS), or they will either not hatch or the larvae will not survive in lake water. The issue then revolves around the question, Is there enough fresh water in these lake microhabitats for cui-ui eggs to produce healthy larvae? This is a difficult question. According to Chatto (1979), from 2 to 3 days are required if hatching is to be successful. LOSL (1982) declare freshly fertilized eggs are intolerant of 5,897 mg/l of TDS, but within a day the embryos have acquired considerable resistance.

Fecundity

Koch (1972) found cui-ui become sexually mature in their fifth or sixth year and produce 20,000 to 30,000 eggs per year. Frazier and Ferjancic (1977) estimated the average-sized female produced 35,700 eggs. Mean number of eggs per female taken at the Marble Bluff facility from 1978 to 1983 was 36,662 (Table 9). This is a nearly linear increase in the number of eggs/female. This may be due to increased efficiency in egg-taking caused by such factors as riper females, better water conditions, better fish-holding facilities, increased use of hormone injections, and/or increased experience of workers (A. Ruger personal communication 1983). The 1983 value of over 55,000 eggs/female may be more indicative of the actual mean fecundity of the species than lower estimates. The 1983 run was quite different from previous years in timing and size of females. Possibly more large females increased the average number of eggs taken. It is understood that, in the wild, a female would have to spawn several times to reach this number, and realistically this may not happen.

Morbidity and Mortality

Large, long-lived cypriniform fishes (such as cui-ui) with relatively small eggs and high fecundity usually experience extremely high mortality rates in their early life stages. At present recruitment is derived from both artificially and naturally reared cui-ui. The hatching success is moderate in the PLF operation, e.g., 75.2% in 1983 (A. Ruger personal communication 1984).

Cui-ui mortality can be divided into five stages: spawning adults, eggs (embryos), larvae, juveniles, and maturing adults. Each stage has differing levels of vulnerability and causes of death. Spawning adults are adversely affected by low flows, high temperatures, and predation. Egg mortality is affected by condition of spawners, high temperatures, and silt. Larvae survival is determined by a complex of factors during their early life in the river, including temperature, flow, food availability, parasites, disease, and predation. In the lake the mortality of juvenile cui-ui is determined by food availability, salinity change, competition, and predation. Nonspawning adults are subject only to mortality factors in the lake environment. Predation

there is minimal; therefore, if food supplies are adequate, then parasites, disease, and senility are probably the most significant adverse factors.

Egg and Larvae Mortality

If the Truckee River spawning habitat were optimal, one would expect high hatching success from the river-spawning cui-ui. However, using the fecundity of 35,700 eggs per female estimated by Frazier and Ferjancic (1977), Scoppettone et al. (1981) projected that if 21 females deposited 750,000 eggs only 20,000 larvae would be produced. Their estimated survival rate to emergence is 2.7%, this was attributed to high temperatures, poor egg viability, and predation by Lahontan redsides, *Richardsonius egregius*.

Adult Mortality

The highest adult mortality probably occurs during the spawning season, when cui-ui are most vulnerable to predation. Historically fishing mortality may or may not have been significant; it continued at low levels, as a snag fishery of spawners on and near the Truckee River Delta, until recent years. Since 1979 all fishing for cui-ui, even by tribal members, is prohibited. Death of adults as a result of spawning, as well as handling mortality during and following egg taking at the Marble Bluff and the PLF facilities occurs at unknown levels. Snyder (1918) reports a few dead individuals along the Truckee River after each spawning season, and high mortality regularly occurred at the mouth of Winnemucca Lake. Fish-eating birds, primarily white pelicans, *Pelecanus erythrorhynchos*, double-crested cormorants, *Phalacrocorax auritus*, and California gulls, *Larus californicus*, can wound or kill adult cui-ui. Although large numbers of white pelicans and cormorants were observed on the Truckee River Delta during the 1976 and 1977 cui-ui spawning migration, Knopf and Kennedy (1980) found no evidence that these birds fed on cui-ui. Common carp, *Cyprinus carpio*, and tui chub, *Gila bicolor*, composed over 97% of the diet of the pelican. T. J. Trelease (personal communication 1984) states he has observed pelicans catch and swallow adult cui-ui. The pelicans then had great difficulty taking off with so heavy a load. He also states he has seen several, but not a great many, cui-ui remains on Anahoe Island. He believes the major damage done by birds is pecking out eyes and gills. Pelicans preyed on adult cui-ui during the large run of 1982 (M. LaFever personal communication 1983). This phenomenon was also observed by D. L. Galat in recent years (personal communication 1984). Snyder (1918) reports that when cui-ui migrate in dense schools considerable numbers are crowded into shallow water and even stranded out of water on sand bars:

> Cormorants, gulls, and pelicans in great numbers were attacking them, and many still wriggling fishes had lost their eyes and strips of flesh had been torn from their sides.

Disease

Pathological studies of the wild cui-ui populations have not been conducted; therefore, the effect of internal and external parasites, fungal infestation, and viral and bacterial disease is unknown.

Effects of TDS on Eggs, Larvae, and Juveniles

Bioassay tests conducted by LOSL (1982) demonstrate the intolerance of fertilized and/or water-hardened cui-ui eggs to TDS concentrations above 525 mg/l. Embryos placed in 525 mg/l water (i.e., Truckee River water) for 24–96 hours survived when transferred to Pyramid Lake water (5897 mg/l), although some abnormalities were found. Embryos placed in 5897 mg/l water immediately after fertilization in 525 mg/l water, were atypical within 24 hours. An average 90% mortality occurred in the 5897 mg/l TDS concentration by the third day, and an average of only 8.3% of the embryos in this concentration produced apparently normal fry.

One-day-old cui-ui larvae placed in test concentrations of either 5781 or 3503 mg/l showed differential mortality; 20% and 13.3% of the test fish died in the respective concentrations within 72 hours. Three day old cui-ui larvae placed in test concentrations of 350 and 5781 mg/l had 100% survival in the first 96 hours. After 192 hours there was no mortality in the 350 mg/l level, but the 5781 mg/l level had 7% mortality and an additional 8% abnormalities.

Chronic 180–day tests indicate that reduced survival of juvenile cui-ui, across a broad range of TDS levels extending from 3620 to

5225 mg/l, represents only 33% to 48% of the 96–hour median tolerance limit (LC50). This indicates that, although LC50 tests may show acute toxicity resulting in death only at high TDS levels, lower TDS levels may cause death or abnormalities when fish are exposed for extended periods of time (LOSL 1982).

HABITAT AND ECOLOGY

Physical

At an elevation of 1154.9 m above mean sea level, Pyramid Lake is approximately 40.8 km long and from 5.8 to 17.3 km wide, with a north-south axis (Fig. 1). At this elevation it has a surface area of 437 km^2, a volume of 25.3 km^3, a mean depth of 57.9 m, and a maximum depth of 100.6 m (Harris 1970). The only significant inflow into the lake most years is the Truckee River, which originates 193 km upstream at Lake Tahoe in the Sierra Nevada. During 1976 and 1977 mean surface temperatures ranged from 6.1 to 23.1 C; the lake is monomictic, thermally stratifying in summer and mixing physically during winter. The most characteristic feature of Pyramid Lake is its high TDS—about 5,350 mg/l during 1976–1977. Although sodium chloride is the dominant salt in the TDS (over 70%), the lake is high in bicarbonate alkalinity that is probably important to the ecosystem. Since the baseload of TDS is relatively constant, the TDS of the lake varies with its volume (Benson 1978b).

Temperature

The maximum surface (0 to 1 m) water temperature in Pyramid Lake was 21.4 and 23.1 C in July 1976 and August 1977, respectively (Lider 1978). The lake is thermally stratified from June through December; wind-generated mixing occurs from January through May. A metalimnion forms at depths ranging from 16 to 22 m. The euphotic depth averaged 11 m for 1976 and 1977, which resulted in a trophogenic zone of about 4.67 km^3 (Galat et al. 1981). Dissolved oxygen (DO) at the surface is always near saturation, about 8 mg/l. Metalimnetic and hypolimnetic DO depletion occurs beginning in July, following stratification and algal decomposition. Maximum DO deficits occur in the profundal zone just prior to fall mixing (Sigler et al. 1983).

Plankton

Diatoms *Cyclotella* sp. and *Stephanodiscus* spp. dominate the phytoplankton community during winter; the most abundant chlorophyte, *Crucigenia* sp., attains its maximum abundance in spring. Blue-green algae are by far the dominate phytoplankton in Pyramid Lake (> 74%). *Nodularia spumigena* is the most abundant blue-green algae. Its bloom begins as early as July and last as late as October. Following spring increases of algal growth, orthophosphate and nitrate are depleted and remain at low levels throughout the summer. Silica, in addition to nitrate, probably limits diatom production in Pyramid Lake (Galat et al. 1981). Chironomids are the lake's most abundant macroinvertebrates, followed by oligochaetes, which are especially abundant in the profundal zone (Robertson 1978). Two euryhaline amphipods, *Gammarus lacustris* and *Hyallela azteca*, are associated with tufa and rocks. La Rivers (1962) reports the Mormon creeper, *Ambrysus mormon*, common among the rocks around the periphery of the lake.

The zooplankton community is composed of five cladocerans, three copepods, and four rotifers (Lider and Langdon 1978). The cladoceran, *Diaptomus sicilis*, is a perennial species and the most abundant zooplankton throughout the year.

Factors Affecting Fish Activity

The cui-ui is the least abundant of the four major fish species native to Pyramid Lake. The other three species in increasing order of abundance are Lahontan cutthroat trout, Tahoe sucker, and tui chub. Vigg (1981) estimates cui-ui compose 0.03% by numbers and 0.47% by weight of the fish population. The mean cui-ui catch/gill net set slightly declined from 1976 to 1977 (1.29 to 0.95). This is not a statistically significant decrease ($P = .21$). During 1982 the largest spawning run in five years ascended the Marble Bluff fishway—13,807 cui-ui (Scoppettone personal communication 1983). Although it is not known what proportion this spawning migration represents of the total adult population, now that the fishway is operational at a near constant efficiency, the magnitude of future spawning

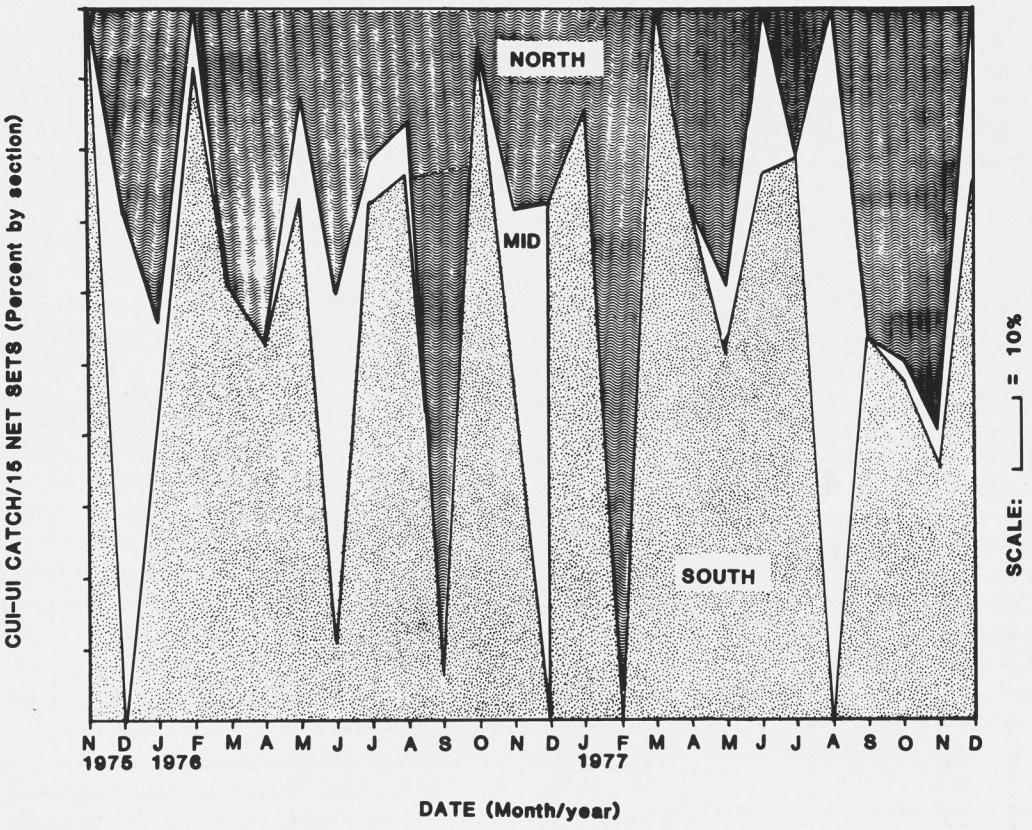

Fig. 8. Proportion of the catch from 15 bottom-set gill nets per month taken in the north (wavy lines), middle (clear), and south (dotted) sections of Pyramid Lake, Nevada, from November 1975 through December 1977.

migrations during years of similar flow regimes will give an indication of cui-ui population trends.

During 1976 and 1977 elevated net catch rates of cui-ui occurred during the spring. There was a concentration in the southern third of the lake during February to May 1976 and March to July 1977 (Fig. 8). Periods of increased proportional catches in the southern section corresponded to a decrease in the relative contribution of the middle third of the lake, with relatively little effect on the catch in the north end. The percent of total was 30, 10, and 60 for the north, middle, and south sections, respectively. The Truckee River delta produced the highest catch rates: 26/net (38.1 m) in May 1976 and 8/net in June 1977. These maxima correspond to the historical spawning period (April to June) and undoubtedly reflect spawning-related activity.

It is a complex of environmental parameters, not just a single variable, that triggers year-round cui-ui activity patterns in Pyramid Lake. We would also expect a multivariate factor to trigger cui-ui spawning runs. Tahoe suckers exhibit a very similar response to the environmental complex in terms of temporal activity (Fig. 9); about 30% of the monthly cui-ui catches can be explained statistically by comparable Tahoe sucker catches ($N = 26$, $P < .01$). This relationship is even more convincing when the spatial effect is included; i.e., 373 individual net samples of the two species in benthic habitats throughout the lake were significantly correlated ($r = .404$, $p < .001$). Thus these two native catostomids are associated in terms of seasonality and habitat.

Environmental variables that can be hypothesized to affect the activity of cui-ui in-

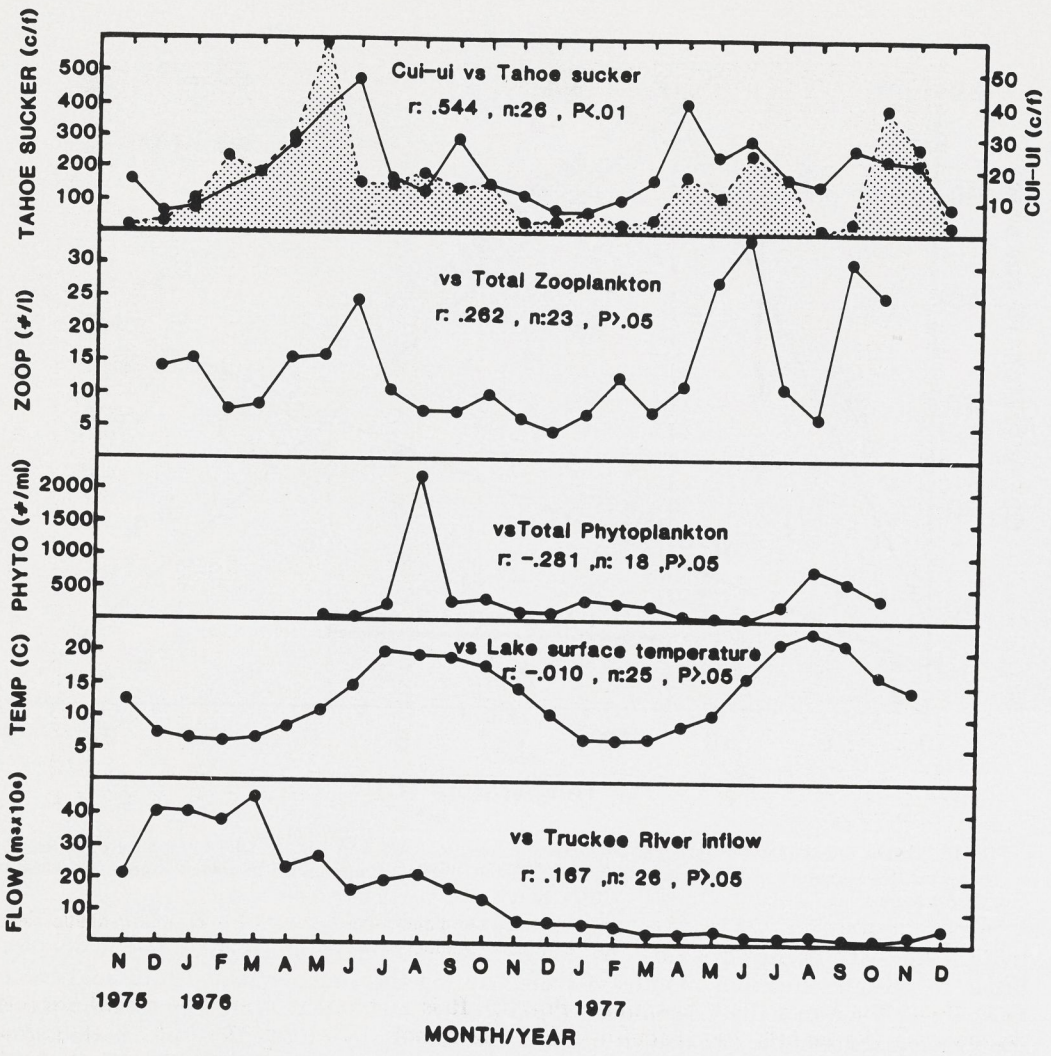

Fig. 9. Comparison of monthly cui-ui catches (shaded) with Tahoe sucker catches, total zooplankton density, lake surface temperature, and monthly Truckee River inflow from November 1975 through December 1977.

clude zooplankton, phytoplankton, lake temperature, and river inflow (Fig. 9). The general pattern of total zooplankton abundance was quite similar to cui-ui activity—unimodal in the spring of 1976 and bimodal in the spring and fall of 1977. The maxima did not correspond exactly, however, and the overall correlation ($r = .262$) was not statistically significant ($P > .05$). Peak phytoplankton concentrations, primarily *Nodularia spumigena*, occurred in June 1976 and August 1977; during these months low numbers of both zooplankton and cui-ui occurred in the samples. The overall correlation between cui-ui and phytoplankton is negative ($r = -.281$) but again not significant. Limited data suggest that cui-ui feed on benthic zooplankton, and *Nodularia* blooms may depress zooplankton populations; therefore these two trophic-related variables may have a cause-effect relationship with cui-ui activity.

It is reasonable to hypothesize that Truckee River inflows affect river spawning-related cui-ui behavior and thus their lakeside activity. The relationship between these variables, however, is very weak ($r = .167$, $P > .05$). The flow regime of 1976 was relatively normal compared to the constant and extremely low flows of 1977. This situation provides an illuminating comparison: in 1976 peak cui-ui ac-

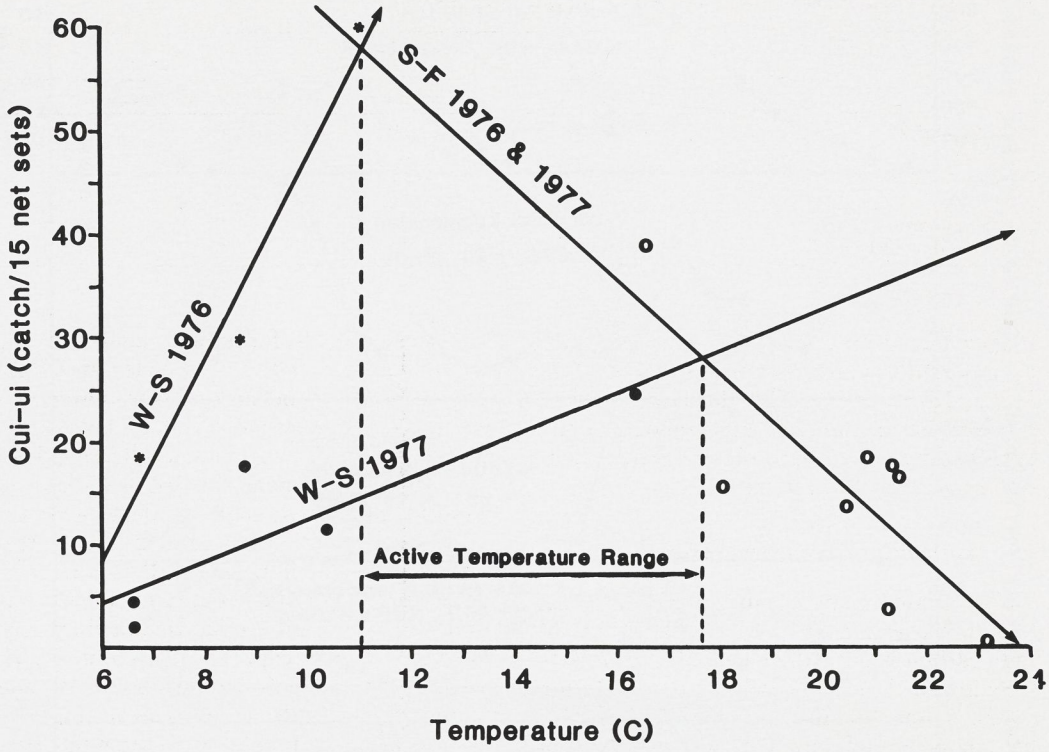

Fig. 10. Direct linear relationships ($P<.05$) between cui-ui catches and surface lake temperature during the winter-spring (W-S) periods of 1976 (asterisks) and 1977 (solid circles) compared to the inverse linear relationships ($p<.05$) during the summer-fall (S-F) periods of 1976 and 1977 combined (open circles).

tivity in the lake occurred in May as flows began to subside after four months of high flows. In 1977 cui-ui activity again peaked in the spring in spite of the fact that river flows had been negligible for over seven months. This limited observation may illustrate that cui-ui have an innate response to spring environmental conditions that is not totally dependent on high river flows. It is notable, however, that the magnitude of the 1977 cui-ui activity peak was much less than 1976 and had a different pattern (bimodal).

Water temperature is another variable that is generally associated with the activity of spring-spawning fishes. There was no linear correlation, however, with lakewide cui-ui activity and the surface temperature of the lake ($r = -.010$, $P > .05$). The explanation for this apparent anomaly is that the relationship is quadratic, not linear. During spring, as water temperature increases from winter minima, cui-ui activity increases in a direct relationship. As temperature continues to increase during the summer past a threshold value, cui-ui catches decline. This relationship is illustrated by Fig. 10; the temperature threshold was 11.0 C in 1976 and 17.6 in 1977. Thus the temperature range of maximum cui-ui activity during the winter-spring period of increase and summer-fall maximum temperature decrease regime was 11.0 to 17.6 during 1976–1977. Photoperiod may also have an (unmeasured) effect on the prespawning migration of cui-ui.

Cui-ui catches varied significantly by season and depth for both 1976 and 1977 ($P < .001$). Maximum densities of cui-ui occurred in the inshore benthic zone from 0 to 15 m in depth, i.e., 2.0 fish/net (Table 10). Catch/effort progressively decreased in benthic areas at depths of 23 and 46 m. No cui-ui was captured at depths 46 m, nor at the surface inshore, nor in the deep water column offshore. These distribution patterns are similar to the Tahoe

TABLE 10. Distribution of 421 adult cui-ui captured in six depth-stratified habitats of Pyramid Lake with experimental gill nets from November 1975 through December 1977 (Vigg 1980).

	Depth (m)	Number of samples	Cui-ui	
			Number	Catch/effort
Inshore benthic:	0–15	199	400	2.01
	23	35	10	0.29
Offshore benthic:	46	152	11	0.07
	46–100	72	0	0
Surface inshore:	0–2	35	0	0
Water column offshore:	0–46	18	0	0

sucker, but according to net catches the cui-ui is apparently more inshore oriented (Vigg 1978a, 1978b, 1980). This does not overlook the fact that in the past large schools of surface-feeding cui-ui were observed over deep water and away from shore.

IMPORTANCE TO NATIVE AMERICANS

Native Americans inhabited the Lake Lahontan ecosystem from at least 11,250 ± 250 radiocarbon years BP, as indicated from artifacts in the Winnemucca Lake basin (Hattori 1982). When the Indians arrived, Lake Lahontan occupied much of western Nevada (Russell 1885, Benson 1978a). Follett (1982) identified remains of four fish species at the Falcon Hill archaeological site, northwest of Winnemucca Lake: cui-ui, Tahoe sucker, Lahontan cutthroat trout, and tui chub; the earliest materials associated with fish remains were radiocarbon dated at 9540 ± 120 radiocarbon years BP. D. R. Tuohy, curator of archaeology, Nevada State Museum, conducted extensive studies of human habitation in the Pyramid Lake basin; his data indicate that between 9500 and 500 BP at least 3 different prehistoric human cultures inhabited the region. The latest culture, the Northern Paiute, live in the vicinity of Pyramid Lake.

The cui-ui at one time constituted the principal food of the Northern Paiute around Pyramid and Winnemucca lakes (Powers 1877). The fact that the Pyramid Lake Paiutes were called kuyuidikadi or kuyuitakuda (eaters of cui-ui) indicates the importance of this fish to the tribe's culture and sustenance. Snyder (1918) reports Pyramid Lake Indians preferred cui-ui to trout. Bath (1978) reports cui-ui were preferred because, unlike trout, they could be dried in the sun and thus preserved for later use. Information collected by Stephen Powers (cited by Fowler and Bath 1981) indicate Tahoe suckers were also eaten regularly, but they were not as favored as cui-ui or trout. For example, a collection from Thea Heye Cave near the southern end of Pyramid Lake contained the desiccated remains of nine or more cui-ui but only one Tahoe sucker (Follett 1977). Pyramid Lake Indians made elaborate adaptations to various components of their wetlands, but they concentrated on the capture of Lahontan cutthroat trout and cui-ui (Harner 1974). The Pyramid Lake Paiutes resisted all attempts by the federal government to turn them into irrigation agriculturalists and instead actively pursued subsistence fishing (Knack 1982).

Elaborate techniques were utilized by Indians to capture fish (Fowler and Bath 1981). Fishing was a year-round subsistence activity at Pyramid Lake and could be separated into river and lake fishing (Bath 1978). River fishing could be further subdivided into (1) exploitation of spawning runs (high water) and (2) low-water fishing. Lake fishing was an individual enterprise practiced during the summer and early fall and accomplished with set lines (for trout), gill nets, harpoons, and spears (Fowler and Bath 1981). However, baited hooks were probably not used for cui-ui. Large treble hooks were utilized at one time to snag cui-ui congregated at the delta.

Cui-ui were caught in large quantities and played an important role in the historic economy of the Pyramid Lake Tribe as a trade item. Follett (1980) reports cui-ui remains at the Karlo Site, about 24 km north of Honey Lake, California. Archaeological sites in Nevada where cui-ui remains have been found include: Humboldt Cave and Humboldt Sink (Hubbs and Miller 1948, Heizer and Krieger

1956), Fishbone Cave and Winnemucca Lake (Orr 1956), Lovelock Cave and Humboldt Sink (Follett 1967, 1970), the Nicolarsen Site at Winnemucca Lake (Follett 1974), Thea Heye Cave at Marble Bluff, Pyramid Lake (Follett 1977), and Falcon Hill (Follett 1982). The Pyramid Lake Tribe was the most widely known band of Northern Paiute. The Paiute name was familiar to Indians from Burns, Oregon, to Owens Lake, California, a distance of more than 805 km (Stewart 1939).

T. J. Trelease (personal communication 1984), who talked to many of the older Paiutes and other local people (some whose observations date back to 1906), believes the cui-ui and trout were taken by Indians in large numbers only during spawning runs. These harvests were so plentiful that they lasted for many months. The tui chub, however, was captured year-round, except during the more severe winter weather, and was a staple in the diet. It was taken from the lake in sagebrush bark nets and by hook and line. Some of the informants Trelease mentioned were Phil Orr, Margaret (Peggy) Wheat and L. W. Morgan.

Spawning runs of cui-ui during high water were fished using platforms with lifting nets, with or without weirs (Fowler and Bath 1981). Sturdy winter platforms were built by several men who shared trout fishing privileges. Spring and summer platforms operated by individuals were less substantial. During summer and early fall, as well as winter, when flow was low and the water clear, harpoons and spears were used (Fowler and Bath 1981). Trelease (personal communication 1984), quoting L. W. Morgan, describes an Indian family fishing expedition sometime between 1906 and 1910 as follows: the father, using a gaff-hook fastened to a long pole, stood in waist-deep water and snagged cui-ui, which were tossed up on the bank. Mother and children built drying racks, cleaned the fish, and put them out to dry. Sometimes platforms were used in conjunction with weirs that directed fish over an area of river bottom paved with white rocks to improve visibility; the lighter bottom also facilitated night fishing.

The fishing technology used by the Walker Lake Northern Paiutes, and at least to some degree by the Carson Lake and Humboldt Basin groups was similar to that of the Pyramid Lake Indians (Speth 1969). Fowler and Bath (1981) conclude native Americans in the western Great Basin have been involved in fishing complexes of various orders and varying degrees for several millenia.

Knack (1982) reports that efficient methods utilized by the Pyramid Lake Paiutes to capture cui-ui and Lahontan cutthroat trout during their spawning runs were unacceptable to the Nevada legislature, which "imposed a definition of appropriate sporting technique, which was derived from the Anglo-European cultural past." Knack (1982) summarized the fishing laws the state of Nevada passed affecting the Indians:

> For over one hundred years, the state of Nevada attempted to impose its laws on the Northern Paiutes of Pyramid Lake. It declared which fish could be caught and where, as well as the techniques to be used. At first, the state tried simply to assume jurisdiction over Indians living on reservations, and then it employed a series of circumventions. Indians were cut off from sales markets and arrested as soon as they left federal trust land. Indian agents were encouraged to enforce state law on the reservation itself. The opportunity to commercialize the one productive resource of the reservation was denied Paiutes by the imposition of state law; economic development was thereby blunted, prosperity stopped, and the local economy allowed to stagnate. Meanwhile, Anglo economic developments, dependent on water diversions to agriculture, mining, and urban areas, produced drastic changes in the fishery population. The state defined fish as a luxury suitable only for sport, and subsequent Anglo actions assured that this would be so.

Trelease (personal communication 1984) strongly disagrees with Knack. He believes the state had only the welfare of the resource in mind, and the federal government, whose responsibility it was, did nothing.

Townley (1980) documents the historical devastation of the Truckee River, the Pyramid Lake trout and cui-ui fishery, and the attitudes of the various sides of the controversy. Snyder (1918) enunciated the attitude of those who believed that the fishery, so important to the livelihood of the Pyramid Lake Indians, could not stand in the way of white man's progress:

> A discussion of the economic value of the fishes of this region and any consideration of methods of propagation and protection must begin and end with the assumption that agricultural and manufacturing interests are of paramount importance. A considerable and constantly increasing amount of the flowing water must be used first for power and then for irrigation, and when any measure intended for the protection of fishes is found to seriously interfere with the working of power plants or the demands of agriculture it will have to be abandoned.

Fortunately for fishery resources in general and the cui-ui in particular, society is evolving a philosophy more compatible with the maintenance of renewable natural resources. Through federal laws, especially the Endangered Species Act, the cui-ui is deemed to be important to society as a whole.

MANAGEMENT

The primary management objective for the cui-ui is the restoration of a stable, naturally reproducing population, thereby allowing its removal from the endangered and threatened species list. This can best be done by increasing numbers substantially and by improving habitat. Ongoing programs designed to reduce man-induced threats to the cui-ui population in Pyramid Lake include: (1) maintenance of water temperatures $\leq$ 13.9 C during spawning, made possible by maintaining adequate flows and shading of the river; (2) renovation of the lower Truckee River so that it has a stable meandering channel and riparian habitat of trees and shrubs; (3) artificial propagation; (4) use of the Marble Bluff Dam and Fishway for monitoring the spawning population, collecting eggs, and providing spawner access to the Truckee River; (5) maintenance of the fishway at Numana Dam to provide spawning access further upriver; (6) continuation of life history studies.

The lower Truckee River temperatures fluctuate with flow, time of day, season, and year. The optimum temperature for cui-ui spawning and egg hatching is 13.9 C. The lower river has a scouring, braided, exposed channel; the need is for a meandering, stable channel and banks that stand firm, with trees and shrubs for shading (Gregory 1982). The impoundment above Marble Bluff Dam has a population of predatory fish including sunfishes and one or more species of catfish. This poses a problem for larval cui-ui that migrate downstream primarily at night. Removal or depletion of predators is a possible answer. In very low water years these larvae may also become disoriented in the impoundment.

The tribe's Pyramid Lake Fisheries organization is rearing millions of cui-ui fry annually, some stocked in Pyramid Lake and in the Truckee River. In 1982, a high water year, more than 11,000 adult cui-ui went up the fishway to spawning sites in the river (13,807 reached the trapping facility). Life history studies have and are exploring stages in the life of the fish and their current and optimum habitat. Artificial propagation should be continued until the number of adult cui-ui in Pyramid Lake is at or near their optimum, if not historic, numbers. Barring disaster, the natural runs should then be able to maintain adequate numbers.

The base load of TDS is essentially static in Pyramid Lake (Benson 1978b). This means the concentration varies inversely with the volume of the lake. The concentration of TDS in Pyramid Lake should not be allowed to increase appreciably; current levels are at or above optimum for cui-ui. The lake levels should not fluctuate beyond a range of plus or minus 3 m except in high water years. Nutrient loading should not be increased from municipal, industrial or agricultural sources.

SUMMARY

The cui-ui, once so abundant that it was a staple in the diet of the Pyramid Lake Paiute Indians and an item of trade, is today endangered. It is a slow-growing, long-lived fish, reaching a length of $>$ 70 cm. Cui-ui eggs must be water-hardened in relatively fresh water. It may or may not be able to spawn successfully in the Truckee River-Pyramid Lake interface, in temporary streams of high water years, or in springs in Pyramid Lake. Biologists are not in firm agreement on these points. Upriver spawning migrations are often, but apparently not always, triggered by surges of fresh water. Spawning starts from mid-April to May and extends through June or, rarely, July.

Modification of the Marble Bluff Fishway provides upstream passage for cui-ui, especially during low water years. Eggs are taken from part of the spawning population; others are allowed to move upstream. Spawning success depends largely on acceptable temperatures and flows. Mortality, primarily from predation, is presumably high on both embryos and larvae in the stream. Once in the lake, young cui-ui undoubtedly face heavy predation. In addition to natural reproduction, millions of larvae are released each year from the David L. Koch Fish Hatchery, Sutcliffe, Nevada.

Cui-ui feed on zooplankton, benthic invertebrates, and algae. They inhabit shallow to medium depth water (< 46 m) in the lake, where they are most active in spring and fall. Adults move into fresh water only to spawn; young cui-ui generally remain in the river for a few weeks after they are hatched.

CONCLUSIONS

The cui-ui is endangered today because of a progressive population decline resulting from transbasin water diversion, failure on the part of the federal government to originally protect the Indians' resources, upstream water use, and early adverse legal and political decisions. Percent of total river flow diversions that began in 1905 reached a climax in the early 1930s, when the combination of low river flows and dropping lake levels caused a delta to form at the mouth of the river. The cui-ui could no longer migrate upstream to spawn; thereafter numbers of adults dropped sharply. To date the population has not stabilized or recovered. Artificial propagation and restoration of river spawning are providing an interim solution. The long-term answer is acceptable spawning habitat: an adequate flow of ≤ 13.9 C water from early to mid-April through June, a stabilized, nonbraided river bed with spawning gravels, and reestablishment of shaded raparian habitat.

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Fish evolution and the late Pleistocene and Holocene history of Clear Lake, California

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ABSTRACT

Clear Lake in Lake County, California, has an endemic fish fauna composed of five lake-adapted forms derived from lowland stream-adapted forms present in surrounding drainage basins. Two of the five endemic forms are extinct. The three remaining endemics maintain themselves despite the destruction of sloughs and tule beds surrounding Clear Lake that are used for spawning and nursery areas. Trophic specializations of the endemic fishes indicate past selection for feeding on small benthic and pelagic invertebrates. The presence of fine particles in the substrate and the reduced activity of tributary streams for at least the past 10,000 yr are major hydrographic features contributing to the evolution of these trophic adaptations.

Subfossil scales of the endemic Clear Lake tuleperch, (*Hysterocarpus traskii lagunae*) present in three U.S. Geological Survey cores (CL-73-7, -6, and -8), removed from the bottom of Clear Lake in 1973 were analyzed by Casteel and others (1975, 1977a, b, 1979) for age and growth rate. Periods of increased scale growth were inferred to represent warming of the lake. Comparison of the Casteel data with pollen data (Adam and others, 1981) indicate that maximum scale growth (core CL-75-8) occurred at about 19 ka (=15 ka, according to Robinson and others, this volume) during a cold interval. Fluctuations in scale density in cores CL-73-4 and CL-73-7, however, seem to follow fluctuations in oak pollen. It is therefore concluded that maximum-scale growth represents cool periods, whereas maximum-scale density represents warm periods in the history of the lake. During the period that maximum-scale growth occurred, Clear Lake basin may have also been closed off from surrounding basins and the lake enriched with nutrients.

INTRODUCTION

The evolution of Clear Lake basin played a major role in the evolution of California fresh-water fishes. The importance of the basin in fish evolution was first realized during an analysis of morphologic variation in the tuleperch (*Hysterocarpus traskii*) (Hopkirk, 1962). The study was prompted by an earlier reference by Tarp (1952) to the existence of a "lacustrine forma" of the tuleperch present in Clear Lake and possibly other lakes of California and a "fluviatile forma" of the same species in the rivers of California. Analysis of the variations in the tuleperch indicated the presence of three subspecies, rather than of two ecologic formae or ecophenotypes: one subspecies is confined to Clear Lake basin, one to the Russian River drainage basin, and one to the remainder of the species range (Sacramento–San Joaquin, San Francisco Bay, and Salinas-Pajaro drainage basins).

Subsequent analysis of other fish species native to Clear Lake basin revealed that at least 5 of the 14 forms then known from the basin were endemic or peculiar to it (Hopkirk, 1967, 1974). The endemic fishes of Clear Lake basin were lake-adapted derivatives of primarily lowland, river-adapted forms found in the Central Valley of California. The extent of differentiation in these fishes indicates that the lake is much older than the few hundred years theorized by Hinds (1952). Taylor (1966) concluded that Clear Lake and Klamath Lake were the only lakes in North America still containing large endemic molluscan faunas similar

Figure 1. Map of Clear Lake, Lake County, California, showing location of 1973 and 1980 core sites (after Rymer and others, 1981). Cores taken in 1973 shown by single-digit numbers. North end of lake shown as it was known to the Pomo Indians (after Kniffen, 1939).

to those that existed during late Pliocene and early Pleistocene time.

In 1973 our knowledge of the history of Clear Lake was vastly improved when the USGS removed eight 12- to 15-cm diameter cores ranging from 13.9 to 115.2 m in length from the lake bottom (Fig. 1). Sims and others (1981) have conclusively shown that the lake is at least 200,000 yr old. If one believes that Clear Lake is a remnant of an ancestral lake represented by deposits of the Cache Formation, then the lake is approximately 1.8 to 3.0 m.y. old (Casteel and Rymer, 1981).

This paper reexamines the fish evolution in Clear Lake basin in light of recent studies on the comparative morphology of Clear Lake fishes and preliminary analyses of material and literature on late Pleistocene and Holocene subfossil fish remains obtained through recent investigations of the paleolimnology of Clear Lake by Sims and colleagues of the U.S. Geological Survey.

NATIVE FISH FAUNA OF CLEAR LAKE BASIN

Clear Lake is presently dominated by introduced species that are characteristic of the low-elevation warm-water areas of the Central Valley of California. The community of fishes found in this type of habitat has been given various names: "fish association one" (Murphy, 1948); "hitch zone" (Hopkirk, 1967, 1974); "introduced fishes association" (Moyle and Nichols, 1973); "deep-bodied fishes zone" (Moyle, 1976); and "introduced warmwater fishes zone" (Moyle and Daniels, 1982).

Historical changes in the fish fauna of Clear Lake are described by Cook and others (1966) and Moyle (1976). Three primary factors caused the decline (or extinction) of native species in the lake: reclamation of peripheral sloughs and channelization of streams for agricultural purposes, removal of tules from around the edge of the lake, and introduction of exotic species.

The drainage of Tule Lake and peripheral sloughs and the destruction of the lower reaches of tributary streams had an adverse effect on species that spawned in those areas, namely the Sacramento perch, Clear Lake tuleperch, thicktail chub, Clear Lake roach, and Clear Lake splittail (the last three species are now extinct). The removal of tules removed the protective cover for young fish (verified by Ralph Holder, an Eastern Pomo Indian who fished the lake in the early 1900s, and by Wendy Jones and Larry Week, biologists for the California Department of Fish and Game). The introduction of exotic fishes provided competitors and predators not present before. Their influence on the native fish fauna is difficult to assess although it must have been substantial.

The following annotated list briefly updates our knowledge of the fishes native to the basin.

Native Fishes of Clear Lake Basin.

Family Petromyzontidae. Lampreys.

***Lampetra tridentata* (Gairdner, *in* Richardson, 1836).** Pacific lamprey. Jordan and Gilbert (1894) reported this species "occasionally taken" in Clear Lake. Ammocoetes recently collected from Kelsey Creek may belong to this species (Taylor and others, 1982); none were seen prior to that time.

***Lampetra pacifica* Vladykov, 1973.** Coast Range brook lamprey ("brook lamprey"). Taylor and others (1982) recorded larval lampreys from the lower sections of Kelsey Creek; Moyle and others (1982) referred to these as brook lampreys. If the Coast Range brook lamprey is native to Clear Lake basin, and there is no reason to doubt it zoogeographically, then the lamprey may possibly represent a new subspecies. Both Coast Range brook lamprey and the Pacific lamprey are present in drainages adjacent to Clear Lake basin.

Family Salmonidae. Trouts.

***Salmo gairdnerii* Richardson, 1836.** Rainbow trout. Rainbow trout occur in every stream and drainage of the basin (Taylor and others, 1982: Fig. 6). They are now rare in the lake. Stone (1874) recorded "trout" in tributaries of the lake and "salmon trout" in the lake itself. "Salmon trout" may have been steelhead from Cache Creek (see Jordan and Gilbert, 1894).

Family Cyprinidae. Minnows.

***Pogonichthys ciscoides* Hopkirk, (1974).** Clear Lake splittail. This endemic species was, until 1940, the most abundant species in the lake. Its abundance was documented by Lindquist and others (1943) and confirmed by Ralph Holder (Hopkirk and McLendon, MS in preparation). The Eastern Pomo name for this species was "hitch," and Kelsey Creek, the major spawning stream for it, was referred to as "hitchbidame" or literally, hitch creek. The Clear Lake splittail was last collected in the late 1960s (Shapovalov and others, 1981).

***Gila crassicauda* (Baird and Girard, *in* Girard, 1854).** Thicktail chub. The thicktail chub, endemic to the Sacramento fish province (see Hopkirk, 1974) and a member of the widespread Western genus *Gila,* was last collected in 1957 in the Sacramento River Delta (Shapovalov and others, 1981). Only two specimens, collected in 1873 and 1938, are known from Clear Lake (Miller, 1963). Based on information provided by Ralph Holder, we know that the thicktail chub or "Indian carp" spawned in sloughs. Along with the black chub, it was often seen in large numbers swimming along the edge of the lake (Hopkirk and McLendon, in preparation).

***Ptychocheilus grandis* (Ayres, 1854).** Sacramento squawfish. Although now rare in the lake, the Sacramento squawfish is still present in fair numbers in the larger exposed sections of Kelsey and Scott Creeks. It was present at 15 (13 percent) of the localities sampled by Taylor and others (1982). In times past, it was undoubtedly better represented in the lake and its tributaries.

***Mylopharodon conocephalus* (Baird and Girard, *in* Girard, 1854).** Hardhead. The hardhead was identified by Casteel, but not emphasized as a new locality record for the basin, in subfossil fish remains from core 8 made by the USGS (Casteel and others, 1979). A fragment of a pharyngeal bone and a tooth of the hardhead were present. Casteel and Rymer (1981) later officially recorded the hardhead from the Kelseyville Formation (Pleistocene) of Clear Lake basin. A pharyngeal bone with teeth intact was recently identified by Hopkirk in material removed from an archeological site north of the exit of the lake into Cache Creek. Because of its widespread occurrence elsewhere, its presence in Clear Lake basin was anticipated (Hopkirk, 1974). When it disappeared from the basin, however, is still unknown.

***Hesperoleucus symmetricus symmetricus* Baird and Girard, *in* Girard, 1854.** Sacramento roach. This species has either been introduced into the basin or represents a recent natural arrival into it: the latter hypothesis may be the correct one. Taylor and others (1982; Fig. 7) found roach at 46 percent of their stream collecting sites. Cook and others (1966) never collected this species from the lake, but did collect it from tributary streams.

***Hesperoleucus grandipinnis* (Hopkirk, 1974) new combination.** Clear Lake roach. This species, considered to be extinct, was formerly placed by Hopkirk (1974) in a new genus and species, *Endemichthys grandipinnis.* Because the name *Endemichthys* Hopkirk, (1974) is preoccupied by *Endemichthys* Forey and Gardiner, 1973, it can no longer be used. Because of certain features that seem to relate it to the genus *Hesperoleucus,* I have assigned it to that genus. The 12 specimens on which the taxon is based do not, as considered by Hubbs (1974) and Coad and Quadri (1978), represent hybrids; the type material consists of males and females with a sexual dimorphism in size (females larger) and in "ripe" condition.

***Lavinia exilicauda chi* Hopkirk, (1974).** Clear Lake hitch. The Clear Lake hitch is at present the most abundant native species in the lake. As mentioned earlier, this species was not the "hitch" of the Eastern Pomo. Their name for this species was

"chigh" (Hopkirk and McLendon, in preparation). Recent workers (Avise and others, 1975; Moyle and Daniels, 1982) have, on the basis of electrophoretic data, decided to merge the genera *Hesperoleucus* and *Lavinia.* Because additional information is needed, my preference is to keep the preceding genera as separate taxa.

***Orthodon microlepidotus* (Ayres, 1854).** Sacramento black chub ("Sacramento blackfish" of other authors). An abundant species in Clear Lake, this species spawns in the lake but not in its tributaries (Cook and others, 1966; Taylor and others, 1982). In other areas of its geographic range, *Orthodon* spawns and survives in low-gradient streams. It is relatively abundant in the Sacramento–San Joaquin Delta. Casteel and others (1977, 1979) found pharyngeal teeth of this species commonly represented in the USGS cores. Casteel and Rymer (1975) also found a pharyngeal tooth of *Orthodon* in the Cache Formation of Clear Lake basin west of the town of Lower Lake. Fossil mammals indicate a late Pliocene or early Pleistocene age for the Cache Formation of Anderson (1936). Pharyngeal teeth of this genus have been found at eight other fossil localities, ranging from Pliocene to late Pleistocene in age, in central California (Casteel and Hutchinson, 1973).

Family Catostomidae. Suckers.

***Catostomus occidentalis occidentalis* Ayres, 1854.** Sacramento sucker. Taylor and others (1982) found suckers widely distributed at lower elevations and in the larger streams of the basin. They were present at 49 (41 percent) of the stream sites sampled. Suckers are at present uncommon in the lake. In times past, however, they were commonly present. In fact, two different spawning populations, stream and lake, may have existed within the basin, comparable to what occurs within the Tahoe sucker (*Catostomus tahoensis*) population of Lake Tahoe (Willsrud, 1971).

Family Gasterosteidae. Sticklebacks.

***Gasterosteus aculeatus microcephalus* Girard, 1854.** Semiarmored threespine stickleback. Taylor and others (1982) found the stickleback only in Cole Creek. Cook and others (1966) reported the collection of two specimens from Clover Creek, near the town of Upper Lake. Based on a very small sample, Kevin Howe (personal communication) found the Clear Lake sticklebacks to have comparatively long dorsal spines. Casteel (1977, 1979) found the threespine stickleback to be the most abundant species, in terms of bone fragments, in USGS cores from Clear Lake. We may be witnessing the demise of an undescribed subspecies with a continuous fossil record of 130,000 yr.

Family Cottidae. Sculpins.

***Cottus asper* Richardson, 1836, subspecies unnamed Hopkirk, (1974).** Clear Lake prickly sculpin. Krejsa (1965) described a number of "phenotypes," actually subspecies, within the species *asper.* Because he was misled by previous records of the riffle sculpin (*Cottus gulosus*) from Clear Lake, based on misidentifications, he failed to consider the prickly sculpin of Clear Lake basin. In 1974, I briefly described the Clear Lake prickly sculpin but did not name it. In their recent survey of the streams of the basin, Taylor and others (1982) did not find either *Cottus asper* or *C. gulosus* at any of their collecting sites. Cook and others (1966) never found *C. asper* outside of the lake. *Cottus gulosus* may be a recent extinction, similar to the hardhead, for the basin. Casteel and others (1977b) found a number of vertebrae and skull bones of *Cottus* (presumably *C. asper*) in core CL-73-6 from Clear Lake. The present population of the prickly sculpin is apparently maintaining itself even though other native species have either declined or disappeared.

Family Centrarchidae. Sunfishes.

***Archoplites interruptus* (Girard, 1854).** Sacramento perch. Although widespread in the fossil record and widely introduced successfully in the West, the Sacramento perch has declined drastically within its original range. It survives in a few isolated farm ponds and localities that are unsuitable for introduced sunfishes. Although now rare in the lake (Peter Moyle, personal communication), it is commonly represented in material from the cores.

Family Embiotocidae. Viviparous Perches.

***Hysterocarpus traskii lagunae* Hopkirk, (1974).** Clear Lake tuleperch. This endemic form is still common in the Blue Lakes and Clear Lake. Baltz and Moyle (1981) recently evaluated the systematics of the tuleperch and confirmed the earlier conclusions (Hopkirk, 1974). Casteel and others (1975, 1977b, 1979), in the analysis of cores from the lake, found the tuleperch to be the dominant species in terms of scales preserved in the bottom of the lake. Based on an age and growth study of the scales, Casteel and others (1977a), concluded that maximum-scale growth was correlated with warm periods in Clear Lake.

Endemic Fishes of Clear Lake Basin

Three of the five endemic forms are members of the minnow family (Cyprinidae): *Pogonichthys ciscoides, Hesperoleucus grandipinnis,* and *Lavinia exilicauda chi.* The first two forms are extinct; our future knowledge of them will therefore be based on museum material and evidence from ethnography, archeology, and paleontology. Because members of the family Cyprinidae are soft-rayed fishes with bones and scales that readily decompose, future knowledge of them from the fossil record will be based primarily on their pharyngeal bones and teeth. The remaining endemic forms are spiny-rayed fishes: *Hysterocarpus traskii lagunae* and *Cottus asper* subspecies. Additional endemic fishes may eventually be described from Clear Lake basin.

TABLE 1. GILL RAKER COUNTS OF LAKE AND RIVER POPULATIONS FROM THE CLEAR LAKE REGION*

Population (Lake/River)	Mean (Sample Size)	Index of Divergence
Gila pectinifer/G. bicolor obesa	32.2(30)/16.7(82) (Lake Tahoe)	1.93
Hesperoleucus grandipinnis/H. symmetricus	15.0(12)/9.0(31) (Central Valley)	1.67
Hesperoleucus grandipinnis/H. symmetricus	15.0(12)/10.2(40) (North Fork, Consumnes River)	1.47
Pogonichthys ciscoides/P. macrolepidotus	21.5(28)/15.8(67) (Central Valley)	1.36
Lavinia exilicauda chi/L. e. exilicauda	28.3(29)/21.4(13) (Russian River)	1.32
Hysterocarpus traskii lagunae/H. t. traskii	23.7(62)/19.0(264) (Central Valley)	1.25
Lavinia exilicauda chi/L. e. exilicauda	28.3(29)/23.5(40) (Central Valley)	1.20
Hysterocarpus traskii laguna/H. t. pomo	23.7(62)/21.9(78) (Russian River)	1.08
Ptychocheilus grandis/P. grandis	11.1(48)/10.9(35) (Central Valley)	1.01
Archoplites interruptus/A. interruptus	29.1(32)/29.0(61) (Central Valley)	1.00
Cottus asper/C. asper	6.4(5)/6.4(9) (Napa River)	1.00
Orthodon microlepidotus/O. microlepidotus	33.2(9)/34.9(33) (Central Valley)	0.95

*Except for Gila, all comparisons are between Clear Lake and surrounding river systems. Gill raker data based on counts made on right first gill arch of preserved material.

All of the endemic forms exhibited what I (Hopkirk, 1974) referred to as lacustrine adaptations. These adaptations were similar to those of other species adapted for living in lakes. They were at one end of the spectrum of adaptations that occurs between populations inhabiting small creeks and populations inhabiting large lakes. Lacustrine adaptations are comparable to pelagic adaptations of "off-shore" marine species. Fluviatile adaptations, those seen in "riverine" or stream fishes, are comparable to benthic adaptations of "in-shore" or bay species.

Endemism in the fishes of Clear Lake basin was attributed to fluviolacustrine speciation. This was one of five possible patterns of geographic isolation and speciation in fresh-water fishes (Hopkirk, 1974). Fluviolacustrine speciation results from the evolution, and subsequent geographic isolation, of a lake on a river system. In the new lake basin, the original river organisms are forced to adapt to a lake environment: more than one lake basin can be evolved, more than one river system can be involved in the process of fluviolacustrine speciation. Based on the extent of the lacustrine adaptations present, and the species that exhibit those adaptations, predictions can be made about how the lake evolved, the age of the lake, and the past ecology of the lake.

TROPHIC ADAPTATIONS OF CLEAR LAKE ENDEMIC FISHES

The morphologic adaptations of fishes can be divided into a number of categories, such as trophic or feeding related, natatory or locomotory, protective or defensive, respiratory, and reproductive. Of the many adaptations seen in the endemic fishes of Clear Lake, trophic adaptations are the most extreme and diagnostic.

Trophic Adaptations

The major adaptive difference between lake and river populations of the Clear Lake region was in a trophic character, the gill raker number (Table 1). Gill rakers sieve food particles from either the water or the substrate, protect the gill filaments, supplement the valvelike action of the gill filaments in separating buccal and opercular chambers, and taste food particles before they enter the esophagus.

The number, shape, length, and spacing of gill rakers relate to the diet of the fish. *Gila* (*Siphateles*) *pectinifer,* a Lahontan basin endemic with extremely fine gill rakers (greatest number of any minnow native to the United States: 29 to 42 counted on the first gill arch), presumably feeds on smaller foods than its river-lake adapted counterpart, *Gila* (*Siphateles*) *bicolor obesa* (Miller, 1951). *G. pectinifer* was confined to the boundaries of pluvial Lake Lahontan and evolved as a lake-adapted derivative of the widespread river species, *Gila* (*Siphateles*) *bicolor.* The origin of the species *pectinifer* antedates the origin of the subspecies *obesa* from *bicolor.* Both *pectinifer* and *obesa* apparently represent lake-adapted derivatives of *bicolor*: *pectinifer* may have originated with the first stage of Lake Lahontan, *obesa* with the third stage of Lake Lahontan.

The systematics of the two species (lake and lake-river) of *Gila* is confused by the occurrence of natural hydridization (sec-

TABLE 2. UPPER AND LOWER JAW LENGTHS OF LAKE AND RIVER POPULATIONS FROM THE CLEAR LAKE REGION

Population (Lake/River)	Mean (Sample Size)	Index of Divergence*
Upper Jaw Length:		
Pogonichthys ciscoides/P. macrolepidotus	63.2 (6)/55.3(10) (Central Valley)	1.14*
Lavinia exilicauda chi/L. e. exilicauda	54.1(8)/47.3(3) (Central Valley)	1.14*
Gila pectinifer/G. bicolor obesa	71.3(10)/70.9(7) (Pyramid Lake)	1.01*
Hysterocarpus traskii lagunae /H. t. traskii	88(56)/87(246) (Central Valley)	1.01
Archoplites interruptus/A. interruptus	152.5(8)/152.1(8) (Central Valley)	1.00
Hesperoleucus grandipinnis/H. symmetricus	68.1(12)/7508(15) (Central Valley)	0.90
Hysterocarpus traskii lagunae/H. t. pomo	88(65)/93(43) (Russian River)	0.95
Lower Jaw Length:		
Pogonichthys ciscoides/P. macrolepidotus	86.8(6)/71.1(12) (Central Valley)	1.22*
Lavinia exilicauda chi/L. e. exilicauda	77.1(11)/66.5(4) (Central Valley)	1.16*
Gila pectinifer/G. bicolor obesa	101.2(10)/97.0(7) (Pyramid Lake)	1.04*

*Lengths given in thousandths of standard length. Measurements are based on preserved material unless noted by an asterisk; those noted by an asterisk are based on dried skeletal material.

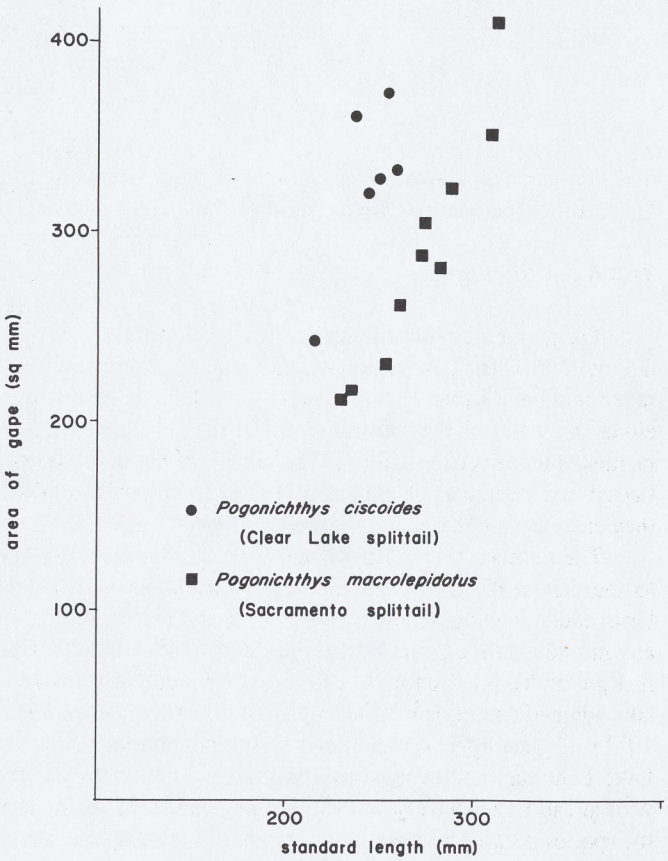

Figure 2. Estimated area of gape in square millimeters plotted against standard length for Clear Lake splittail (*Pogonichcthys ciscoides*) and Sacramento splittail (*P. macrolepitodus*).

ondary and introgressive) between the two forms in areas of sympatry. Gene flow from *pectinifer* to *obesa* through fertile F_1 hybrids is common in a number of lakes. However, as Carl Hubbs (1961) pointed out, the two forms are remarkable in maintaining their genetic integrity. Needless to say, reproductive mechanisms isolating the two forms are poorly understood. The great similarity in body shape and color often seen between the two forms is the result of introgressive hybridization, a beneficial process that allows the survival of a stream form (*bicolor obesa*) in an environment now deficient in streams.

Unlike the two forms of *Gila* in the Lahontan basin, the lake-adapted form (*ciscoides*) of *Pogonichthys* is essentially geographically isolated from its river congener (*macrolepidotus*) of the Sacramento River system. In terms of trophic adaptations, *ciscoides* parallels other lake-adapted minnows in possessing fine gill rakers (Table 1), long lower and upper jaws (Table 2) and therefore a larger gape (Fig. 2), and small pharyngeal arches (Table 3). Although advanced in the preceding features, the genus *Pogonichthys* still retains the primitive feature of two rows of teeth on each pharyngeal arch. The inner row of teeth is present in almost all cyprinid genera; the outer row, however, is reduced or absent in lake-adapted forms and in microphagous species (Table 4). A second evolutionary trend is for an increase in the number of inner row teeth, as seen in *"Endemichthys," Orthodon, Lavinia,* and *Gila* (*Siphateles*) (Table 4).

The increased jaw length in the lake minnows indicates that a greater volume of water (and plankton) can be taken in and passed over the gill rakers. The reduced pharyngeal arch implies that smaller foods (prey organisms) are represented in the diet of lake minnows. Even *Hysterocarpus,* a member of a completely different order of fishes, reveals the same evolutionary trend in the reduction of the pharyngeal arch. The Clear Lake tuleperch has a reduced surface area on the inferior pharyngeal arch for grinding up food (Fig. 3).

Hubbs and others (1974) emphasized the conservative nature of gill rakers. Once evolved, lacustrine types with many gill

TABLE 3. LENGTH, WIDTH, AND HEIGHT OF LOWER PHARYNGEAL ARCH IN LAKE AND RIVER POPULATIONS FROM THE CLEAR LAKE REGION*

Population (Lake/River)	Mean (Sample Size)	Index of Divergence*
Lower Pharyngeal Length:		
Pogonichthys ciscoides/P. macrolepidotus	65.3(38)/69.6(41) (Central Valley)	0.94
Gila pectinifer/G. bicolor obesa	81.3(20)/86.9(11) (Pyramid Lake)	0.94
Lavinia exilicauda chi/L. e. exilicauda	64.3(20)/68.8(40) (Central Valley)	0.93
Lower Pharyngeal Height:		
Pogonichthys ciscoides/P. macrolepidotus	51.0(20)/55.5(40) (Central Valley)	0.92
Gila pectinifer/G. bicolor obesa	42.8(35)/48.9(42) (Central Valley)	0.88
Lavinia exilicauda chi/L. e. exilicauda	54.2(20)/67.2(11) (Pyramid Lake)	0.81
Lower Pharyngeal Width (including teeth):		
Pogonichthys ciscoides/P. macrolepidotus	45.7(20)/48.3(40) (Central Valley)	0.95
Gila pectinifer/G. bicolor obesa	34.2(38)/38.3(42) (Central Valley)	0.89
Lavinia exilicauda chi/L. e. exilicauda	43.1(19)/53.3(10) (Pyramid Lake)	0.81

*Measurements given in thousandths of standard length (made with the aid of dial calipers). All measurements based on dried skeletal material.

TABLE 4. PHARYNGEAL TEETH OF LAKE AND RIVER POPULATIONS FROM THE CLEAR LAKE REGION

Population (Lake/River)	Mean (Sample Size)	Index of Divergence*
Outer Row (total no.):		
Pogonichthys ciscoides/P. macrolepidotus	1.36(44)/1.72(32) (Central Valley)	0.79
Both Arches (total no.):		
Hesperoleucus grandipinnis/H. s. symmetricus	10.2(12)/9.0 (Moyle, 1976) (Central Valley)	1.13
Lavinia exilicauda chi/L. e. exilicauda	10.0(13)/9.9(30) (Central Valley)	1.01
Gila pectinifer bicolor obesa	9.0(30)/9.1(29) (Lake Tahoe)	0.99
Pogonichthys ciscoides/P. macrolepidotus	12.64(22)/13.50(16) (Central Valley)	0.94

rakers are "slow" in undergoing an evolutionary reduction in number. The preceding authors cited (p. 146) as an example of this the Mohave tuichub, *Gila bicolor mohavensis* (Snyder, 1918), a lake derivative of *bicolor* adapted for pluvial Lake Mohave, which has persisted under postpluvial conditions that are conducive to fluviatile types (Hubbs and Miller, 1943).

Paleolimnologic Implications

Increased gill raker number and length, increased jaw length (hence increased gape), reduced dentigerous surface of the inferior pharyngeal bone, decreased height of the inferior pharyngeal bone, and a reduction in the number of pharyngeal teeth, as shown in the preceding tables and figures, suggest a prolonged period of selection for microphagy (feeding on small prey) in Clear Lake. The evolutionary progression toward microphagy means that a greater volume of water or substrate must be filtered. This requires a larger gape and a more active life style. A more active life style is indicated by an increase in the number of gill filaments (Hopkirk, 1967). Those species most influenced have been those feeding on zooplankton and small benthic insect larvae (mostly dipteran). Piscivores (Sacramento perch, Sacramento squawfish) and phytoplanktivores (Sacramento black chub) exhibit no great differences in trophic adaptations in Clear Lake.

The adaptations seen in the Clear Lake endemics thus lead to the assumption that Clear Lake has been completely or partially isolated from surrounding basins for long enough (late Pleistocene and Holocene time) for speciation to have occurred. The lake has been subjected to sedimentation (mostly clay, silt, and volcanic ash) and eutrophication for a long period of time; complete filling-in of the lake never occurred because of continued subsidence of the basin (Sims, 1976). Fine sediment has continually provided a substrate for dipteran larvae (Clear Lake is notorious for one of them, *Chaoborus astictopus,* the Clear Lake gnat), tules, and tule-associated organisms, and has created marshes and peripheral sloughs.

The endemic fish fauna of Clear Lake is not restricted to

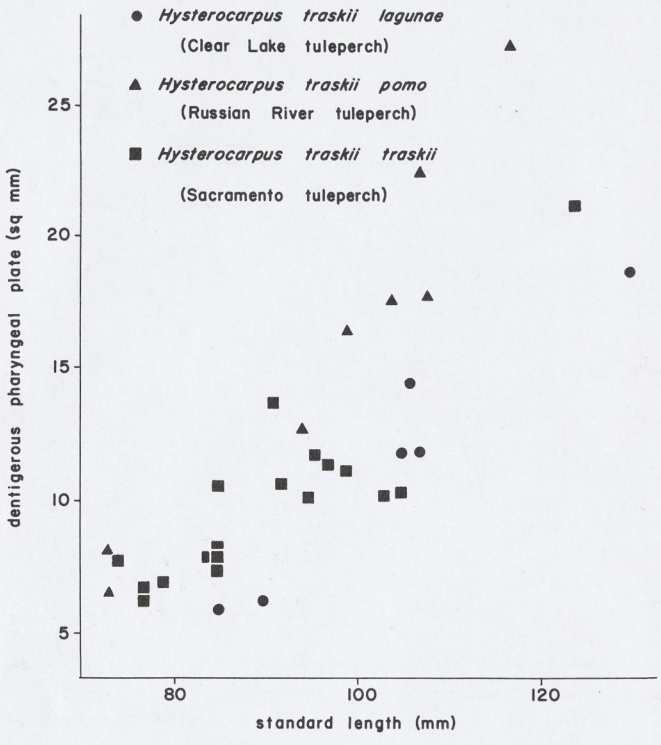

Figure 3. Surface area in square millimeters of dentigerous, or tooth-bearing, pharyngeal plate in the three subspecies of the tuleperch (*Hysterocarpus traskii*) (after Hopkirk, 1967).

Clear Lake but is also found in the Blue Lakes (Fig. 1) and other subbasins within the basin. Although fishes of the Blue Lakes diverge slightly from those of Clear Lake, they definitely belong to the Clear Lake population in terms of taxonomy. The amount of isolation and evolutionary divergence between the Blue Lakes and Clear Lake fishes is comparable to that seen between Lake Tahoe and Pyramid Lake fishes (Hopkirk, 1974).

Strong-flowing cold streams have not existed in the basin for thousands of years. Conspicuously absent from the basin are the riffle sculpin and the speckled dace. Both species are found in cold tributaries of Cache and Putah Creeks, immediately east of Clear Lake basin.

Fluviolacustrine speciation, considered previously as the type of geographic speciation responsible for the Clear Lake endemic fish fauna, is in the final analysis the product of substrate selection. In this example of substrate selection, however, fine particle size selects primarily for small interstitial organisms. Concealing coloration is of secondary importance. Benthic-feeding river fishes, when introduced into a lake environment, experience selection toward microphagy and planktiphagy, especially if tributary streams to the lake become inactive or intermittent. This type of selection has produced the endemic fishes of Clear Lake, Lake Biwa, and many other lakes characterized by a long history of fine-grained sedimentation.

SUBFOSSIL TULEPERCH SCALES AND THE PALEOLIMNOLOGY OF CLEAR LAKE

Fish bones and scales have been analyzed from a number of the 1973 Clear Lake cores, although fish bones and scales in the 1980 cores have yet to be analyzed. Casteel has analyzed fish subfossils from three of the cores removed in 1973: core CL-73-7 (Casteel and others, 1975, 1977a), core CL-73-6 (Casteel and others, 1977b), and core CL-73-8 (Casteel and others, 1979). I have analyzed scales, separated by the USGS, from the upper layers of core CL-73-4. Sims (1976) has described the physical features of the cores removed in 1973.

Preservation of Subfossil Fish Remains

Fish scales are represented in the last 25,000 yr of the cores examined so far. Unfortunately, the scales that are present represent only a limited portion of the total fish fauna. Most scales are those of the Sacramento perch and the Clear Lake tuleperch. These two species represent approximately one-eighth of the original fish fauna. Scales from the soft-rayed species, which composed the bulk of the biomass and the fauna, are rarely present and then appear only in the form of curled shreds. Conditions for preservation were adverse for scales with a low percentage of bone. Scales of the tuleperch are apparently ideal for preservation and often appear entire. Sacramento perch scales, on the other hand, are so bony and brittle that they usually appear as fragments.

Environmental conditions in shallow arms of the lake, as seen in cores CL-73-6 and -7, resulted in peat formation that may have destroyed many scales (see Casteel and others, 1977a). Preservation of tuleperch scales in core CL-73-7 was decidedly poor in comparison to preservation in cores CL-73-6 and -8. Core CL-73-7 has a preservation rate of 0.008 scales/yr, core CL-73-6 a rate of 0.016 scales/yr, and core CL-73-8 a rate of 0.025 scales/yr. The preceding rates are based on tuleperch scales present in the cores for roughly the last 11,000 yr.

Fish bones are usually fragmented and not especially common. Those seen are primarily those of the threespine stickleback. A few pharyngeal bones and teeth of tuleperch, minnows, and suckers are also seen.

Age and Growth Studies of Subfossil Tuleperch Scales

Casteel and others (1975, 1977b, 1979) aged subfossil scales of the tule perch, measured distances between year rings or annuli, and then estimated standard lengths in millimeters and weight in grams of the fish at the end of each year of growth or annulus. On the basis of age and growth data from core CL-73-7, the first core analyzed, Casteel and others (1975, 1977a) hypothesized that scale growth was essentially dependent on tempera-

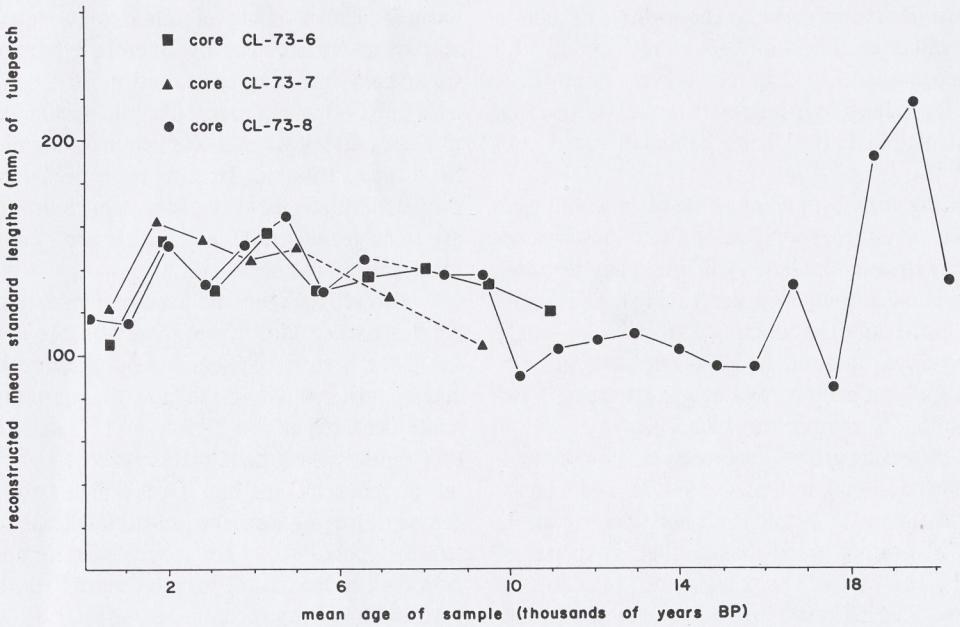

Figure 4. Reconstructed mean standard lengths of age class 3 tuleperch (*Hysterocarpus traskii*) plotted against mean age of core sample in thousands of years BP (based on data of Casteel and others, 1975, 1977b, 1979).

ture. It was inferred that warming of the lake began about 10 ka and ended about 2.8 ka. A marked period of warming occurred between about 4 ka and 2.8 ka. These findings appeared to be consistent with tree-line studies and palynology (Adam, 1967; La Marche, 1973).

Additional age and growth studies of subfossil tuleperch scales from cores CL-73-6 (Casteel and others, 1977b) and CL-73-8 (Casteel and others, 1979) augmented paleoclimatic trends reconstructed earlier from core CL-73-7. Based on the past 12,000 yr (8,000 years according to Robinson and others, this volume), scales from core CL-73-6 (Oaks Arm of the lake) exhibited the greatest average growth for fish in their first two years of life; core CL-73-8 (open-water area opposite the mouth of Rodman Slough), the least growth. Core 8 provided a longer history of tuleperch growth (and inferred temperatures) than did cores CL-73-6 and -7 (see Fig. 4). Age classes 1 and 2 exhibited their smallest estimated standard lengths during the latest Pleistocene (ca. 15 ka, or 11 ka of Robinson); age class 3 of core CL-73-8 had its smallest estimated standard length at about 17 ka (13 ka of Robinson). Core CL-73-8 had extraordinary growth at about 19 ka (15 ka of Robinson); the estimated standard length was 219 mm (Fig. 4). Even in the best environments (Sacramento Delta), the growth at the end of the third year in present populations is only about 150 mm in standard length.

A second possible explanation of growth rates in subfossil tuleperch scales is eutrophication. During the interval when growth was maximum in core CL-73-8, Kelsey Creek was actively bringing nutrients into the lake from the surrounding watershed. Clear Lake was ending a pluvial period comparable to that experienced by Lake Lahontan (see Benson, 1978). If we use the corrected radiocarbon datings of Robinson and others (this volume), Clear Lake was in the "late-glaciation transition" stage of Adam and others (1981). Fluctuations in scale growth seen in Figure 4 do not relate to fluctuations in oak pollen abundance (inferred warming) but instead to the fluctuations in abundance of pine and TCT (Taxodiaceae, Cupressaceae, and Taxaceae) pollen (inferred cooling).

The optimum water temperature for the tuleperch may well be much colder than previously thought. The tuleperch, as the only fresh-water member of a cold temperate marine family (Embiotocidae), would probably do well in moderately cold alkaline water. During the drought of 1976–1977 in California, the Russian River tuleperch became the dominant species in the alkaline Sonoma State University Pond (Rohnert Park, California), suppressing the introduced centrarchids. The Sacramento perch, an ecologic associate of the tuleperch and a native centrarchid, has been successfully introduced into a number of alkaline lakes in Nevada and elsewhere in the Great Basin (La Rivers, 1962; Moyle, 1976). Growth of the Sacramento perch is significant in these interior lakes.

Eutrophication of Clear Lake, if coupled with a closure of the drainage basin, would have resulted in a spectacular growth rate. Conversely, a dramatic opening of the basin to the Sacramento River system would have resulted in a drastic loss of

nutrients and a sharp decline in growth. The greatest decline in growth occurred at either ca. 17.55 or 15.7 ka (13.35 and 11.5 ka, if corrected), depending on which age class is examined. A second explanation for a sharp drop in growth would be the rapid decline of a pluvial period. Pluvial Lake Lahontan lasted until 11.1 ka (Benson, 1978).

Besides influencing growth, opening of the basin would have allowed stream species to either repopulate basin streams or genetically merge with any stream population still present in the basin. A gradual reduction in the amount of water leaving the basin and a gradual increase in the nutrients coming into the lake would have resulted in a gradual increase in Holocene scale growth. Fluctuations within this gradually increasing growth trend, however, were brought about by temperature changes.

In conclusion, increasing growth rates seen in subfossil tuleperch scales may reflect declining water temperatures and increasing eutrophication. An increase in tuleperch scale density in the cores may indicate a warming trend that resulted in successful spawning and survival of young. The consequence of successful reproduction, however, would have been an increase in intraspecific competition and a decrease in growth rate. The small size of these tuleperch would have increased their vulnerability to the Sacramento perch and allowed that species to increase in size. A future age and growth study of the subfossil scales of the Sacramento perch from the USGS cores of Clear Lake is necessary to validate the latter hypothesis.

SUMMARY

Trophic adaptations in the endemic fishes of Clear Lake basin indicate a reduction in macroinvertebrates in the substrate and their replacement by microinvertebrates. The bottom of Clear Lake has been composed mostly of fine sediments for at least 130,000 yr. A coarse substrate developed around the mouth of Kelsey Creek when it was active during the last glacial period. Since then, tributary streams have been intermittent and have provided little in the way of a stream environment. An evolutionary trend from benthic macrophagy to benthic microphagy and planktiphagy has occurred.

Growth data derived from previous studies of subfossil tuleperch scales obtained from three USGS cores (CL-73-7, -6, and -8) of the bottom of Clear Lake suggest changes in temperature and in nutrients within the lake. Maximum estimated growth of scales occurred at about 19.4 ka (15.2 ka of Robinson) during a time period when the climate was cool and humid (indicated by the presence of pine and TCT pollen), and Kelsey Creek was actively bringing nutrients into the lake and providing a coarse stream-type substrate for macroinvertebrates. During the time period when maximum growth occurred, the basin may also have been isolated from surrounding basins.

ACKNOWLEDGMENTS

I am grateful to John D. Sims for inviting me to leave the classroom to again become active in studying the past history of Clear Lake and its fascinating endemic fishes. I leaned heavily on the creative endeavors of others, primarily Richard W. Casteel, David P. Adam, Michael J. Rymer, and John D. Sims, and thus I wish to acknowledge the contributions they have made to our understanding of the history of Clear Lake.

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Impact of a major soil fumigant spill on the planktonic ecosystem of Shasta Lake, California

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Abstract: On July 14, 1991, approximately 70 000 L of the soil fumigant Vapam®, metam sodium, was spilled into the upper Sacramento River, California. Twelve hours before this spill reached Shasta Lake we sampled several sites in a subsequently impacted area and two control stations. Thereafter, samples were collected at approximately 5-d intervals for 26 d. We observed an almost immediate and subsequent 99.9% decrease in zooplankton biomass within 2.0 km of the river inflow. Lake-water chlorophyll concentrations crashed immediately to 20% of prespill values, but rebounded to approximately 750% prespill values after 9 d as a result of a spill-driven diatom bloom. Dissolved inorganic nitrogen and phosphorus concentrations increased severalfold immediately after the spill but returned to prespill concentrations as the algal bloom peaked. Effects of the spill were clearly related to distance from the river inflow with strong effects observed within 2.0 km, and weak or no effects observed at 8.0 km into the reservoir. A dilution experiment, using varying mixtures of contaminated and control station lake water, strongly confirmed the principal findings of the field study. Our field and experimental data showed far more severe effects of the spill than single species bioassays and lake pesticide concentrations predicted.

Résumé : Le 14 juillet 1991, 70 000 L environ d'un agent de fumigation de sol, le Vapam®, ou métam-sodium, ont été déversés par accident dans le cours supérieur de la rivière Sacramento, en Californie. Douze heures avant que le produit n'atteigne le lac Shasta, nous avons procédé à des prélèvements en plusieurs sites, qui ont ensuite été contaminés, ainsi qu'à deux stations témoins. Des échantillons ont ensuite été prélevés à intervalles de 5 jours environ pendant 26 jours. Nous avons noté une chute presqu'immédiate de 99,9% de la biomasse du zooplancton dans un rayon de 2,0 km du point d'affluence de la rivière dans le lac. La concentration de chlorophylle des eaux du lac a chuté immédiatement de 20%, par rapport à la valeur d'avant le déversement, mais elle s'est ensuite rétablie pour atteindre 750% de cette valeur 9 jours après le déversement, suite à une pullulation des diatomées s'expliquant par le déversement. Les concentrations d'azote et de phosphore inorganiques dissous ont augmenté de plusieurs fois immédiatement après le déversement, pour ensuite se rétablir aux valeurs d'avant le déversement, au moment où la pullulation d'algues atteignait son maximum. Les effets du déversement étaient nettement fonction de la distance du point d'affluence de la rivière. Les effets les plus importants ont été notés dans un rayon de 2,0 km tandis qu'à 8,0 km de ce point, les effets étaient faibles ou indécelables. Un essai de dilution portant sur divers mélanges d'eau du lac contaminée ou provenant de la station témoin a permis de confimer les principaux résultats de l'étude sur le terrain. Nos données, tant celles obtenues sur le terrain que les données expérimentales, ont montré que les dommages causés par le déversement étaient beaucoup plus importants que ceux que permettaient de prévoir les bioessais portant sur une seule espèce ou les concentrations de pesticides mesurées dans les eaux du lac.

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Introduction

A train derailed near Dunsmuir, Calif., on July 14, 1991, releasing approximately 70 000 L of the soil fumigant Vapam® into the upper Sacramento River. Initial findings indicated that almost all aquatic animal life was killed in the upper Sacramento River from the site of the train derailment to the river's terminus at Shasta Lake (CDFG 1993). In this investigation we describe this spill's effect on the planktonic ecosystem of Shasta Lake (Fig. 1), California's largest reservoir, which is located approximately 55 km downstream from the original spill site.

Vapam®, 33% metam sodium (sodium methyl dithiocarbamate) in aqueous solution, is a monoalkyldithiocarbamate fungicide. This class of pesticides is highly toxic to fungi, plants, and animals (Pimentel 1981; CPCR 1990). When combined with water metam sodium hydrolyzes to form the gas methyl isothiocyanate (MITC). The isothiocyanate group is the active agent of metam sodium (Pimentel 1981; CPCR 1990). Although this class of pesticides is known to be extremely toxic and metham sodium is one of the most widely used pesticides in the United States (Alvarez and Moore 1994), apparently no data describing metham sodium's toxicity to aquatic or terrestrial ecosystems have been published.

The pesticide plume was measured at 14 000 μg/L MITC at the Sacramento River outflow when it first entered Shasta Lake. However, this extremely concentrated plume dissipated rapidly because of dilution and volatilization in Shasta Lake (CRWQCB 1991) (Fig. 2). MITC concentrations above 100 μg/L were only noted within 1 km of the river inflow during the first 48 h after the spill, and concentrations above 1 μg/L, the limit of detection, were only sporadically observed farther than 8 km from the river inflow or more than 10 d after the spill entered the lake. The very rapid loss of MITC from Shasta Lake is consistent with del Rosario et al.'s (1994) finding that MITC's parent compound metam sodium dissipated very rapidly from tap water.

While many studies have examined the toxicity of pesticides in single-species laboratory bioassays, or measured the presence and fate of these compounds in nature, far fewer investigations have actually documented the effects of these compounds on natural ecosystems. Of those investigations concerning ecosystem level effects, most have been terrestrial studies (Cairns 1990). Of the aquatic investigations, most have examined stream ecosystem responses, particularly the responses of stream insects and fishes, with very few studies examining how lake plankton communities respond to these perturbations (Niemi et al. 1990).

Complex systems are perturbed at much lower concentrations of pesticides than single-species bioassays would suggest (Lampert et al. 1989; Stay et al. 1989). For example, Lampert et al. (1989) found 10 000 μg/L atrazine was required to cause acute toxicity (50% mortality after 48 h) for *Daphnia*, while approximately 2000 μg/L atrazine was required to cause significant reductions in *Daphnia* feeding, growth, and reproduction. However, 100 μg/L atrazine caused a significant reduction in *Daphnia* population size in an "artificial food chain" and natural planktonic communities showed significant responses to atrazine at concentrations as low as 1 μg/L (Lampert et al. 1989). The concentrations at which these compounds elicit toxic effects and the persistence of these effects varies greatly from compound to compound. Several investigations have examined the effect of more commonly used pesticides on aquatic environments, but to our knowledge, no one has previously documented metam sodium effects on aquatic, or any other, ecosystems.

We collected water samples from Shasta Lake approximately 12 h before the spill arrived and at regular intervals thereafter for 26 d. In addition, we conducted a dilution series experiment, using mixtures of contaminated and control station lake water, immediately after the spill entered Shasta Lake. This experiment was designed to predict what effect this spill would have on Shasta Lake biota and to aid in interpreting our field results.

Methods

Field sampling

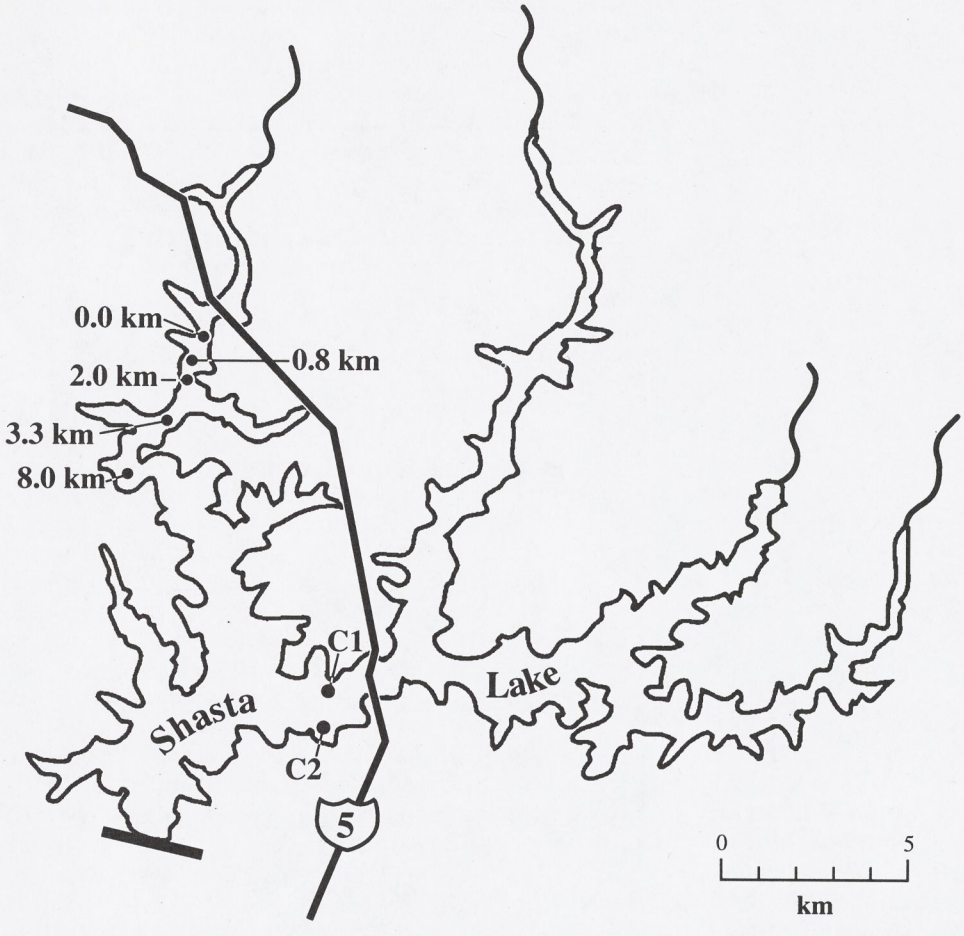
During the 48 h it took for this spill to reach Shasta Lake we collected samples for determination of dissolved oxygen (DO), dissolved inorganic nitrogen (DIN; ammonium, nitrate, and nitrite), soluble reactive phosphorus (SRP), and chlorophyll *a* (Chl) concentrations and zooplankton biomass from three stations (0.0, 0.8, and 2.0 km) within the impacted arm of Shasta Lake (Sacramento River arm) and from two stations (controls 1 and 2) in an unaffected arm of the reservoir (Pit River arm) (Fig. 1). Thereafter, the same series of samples was collected at 0.0, 0.8, 2.0, 3.3, and 8.0 km from the Sacramento River – Shasta Lake junction, as well as at the Pit River arm control stations. These samples were collected 12 h before the spill reached the reservoir and 1, 5, 9, 15, and 26 d after impact.

During each sampling event we collected one composite sample at each station by pooling samples collected from several depths. When the station was less than 8 m deep we pooled samples from 1-m intervals. When the station was ≥8 m deep we pooled water at 2-m intervals to form a 0- to 8-m surface composite sample. Water for DIN, SRP, Chl, and phytoplankton analyses was collected with a Van Dorn sampler. Water for DIN, SRP, and Chl analyses was filtered immediately after collection with a 200-μm mesh screen to remove large zooplankton. Water for phytoplankton enumeration was left unscreened and preserved immediately with Lugol's solution. The water chemistry samples were stored on ice until analysis. Zooplankton was sampled at the same depths as the water chemistry samples, using a 12.5-L Schindler trap with a 63-μm mesh. The zooplankton samples were preserved immediately with a 1% Lugol's and sucrose solution.

Dissolved oxygen (DO) and temperature were measured at 1-m intervals using a Yellow Springs Instruments (YSI) DO Probe. We calibrated our DO probe against the Winkler method on July 22, 1991, at which time we obtained a very good agreement, i.e., YSI values averaged 103 ± 5.5% (mean ± SD; $n = 5$) of Winkler estimates. After noticing a pronounced DO minimum at 3.3 km on July 22, we collected a vertical profile at this station by taking water for nutrient and chlorophyll analyses at 1- or 2-m intervals.

On the day before the spill entered Shasta Lake, July 16, 1991, we were unable to begin sampling until 16:00 because

Fig. 1. Shasta Lake, north central California, and an outline of its shoreline when at full capacity. The approximate locations of the impacted and control stations are indicated by the station names on the map. The location of the first impacted station (0.0 km; Sacramento River inflow) does not correspond to the outline of Shasta Lake's shoreline because the reservoir was only at 50% capacity when the spill occurred.



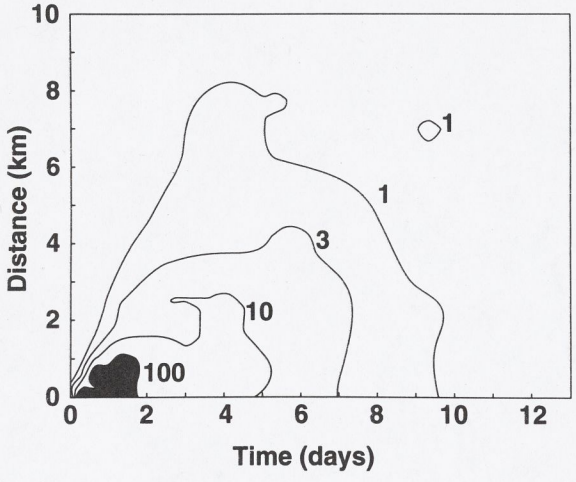
of delays in gaining authorization to collect samples. We were, therefore, only able to obtain initial samples at five stations. On July 18, we added two lake stations (3.3 and 8.0 km) to our initial five stations. On July 22 we were unable to sample both control stations because of severe winds on the lake. On July 26 and August 1, we sampled all seven stations. Because of lowering of the surface level of Shasta Lake, we lost our 0.0 km station on August 12. Unless explicitly stated otherwise, days after the spill refers to the number of days after the spill entered Shasta Lake and not to the date of the actual train derailment on the upper Sacramento River.

Dilution bioassay

An in situ dilution experiment was conducted by mixing lake water collected on July 18, 1991 (1 d after the spill entered Shasta Lake), from stations 0.0 km and control 2. The treatments used were 50, 13.5, 3.5, 1, and 0% contaminated lake water mixed with lake water from control station 2. The experiment was started on July 19 and terminated 8 d later on July 27, 1991. Twenty-litre Cubitainers (semitransparent plastic bags) were used as experimental vessels, each treatment had four replicates, and the Cubitainers were incubated at 5 m depth in Castle Lake, California (site of the University of California, Davis, Limnological Research Station). It was impossible to incubate our experiment in Shasta Lake because of logistical considerations. The Cubitainers were incubated at 5 m depth to avoid photoinhibition of algal growth and to mimic light intensity at the depth of collection in Shasta Lake. During the experiment the temperature at 5 m in Castle Lake was approximately 19°C, which was several degrees cooler than the 26°C surface waters of Shasta Lake. The lower temperature would, however, only be expected to make the results more conservative by lowering the metabolic rates of the plankton.

Water samples for analysis of MITC were collected from the dilution bioassay on experiment days 5 and 8 in 1-L dark amber bottles. These samples were collected with no air being allowed in the bottles and stored at 4°C for 24 h at which time they were transported for final processing and analysis. At the end of the experiment a 1-L sample was collected for DIN, SRP, Chl, and phytoplankton analyses, and treated in the same manner as the field samples.

Fig. 2. Contour isopleth of measured MITC concentrations (μg/L) in Shasta Lake (CRWQCB 1991). This figure was obtained by taking means of 50 independent distance and time vertical sample profiles and kriging (an averaging algorithm) logarithmic transformed data by date and distance. From 0 to 4 d, CRWQCB sampling was concentrated from 0 to 2.5 km into Shasta Lake, while from 4 to 13 d sampling was concentrated from 2.0 to 8.0 km into the reservoir.

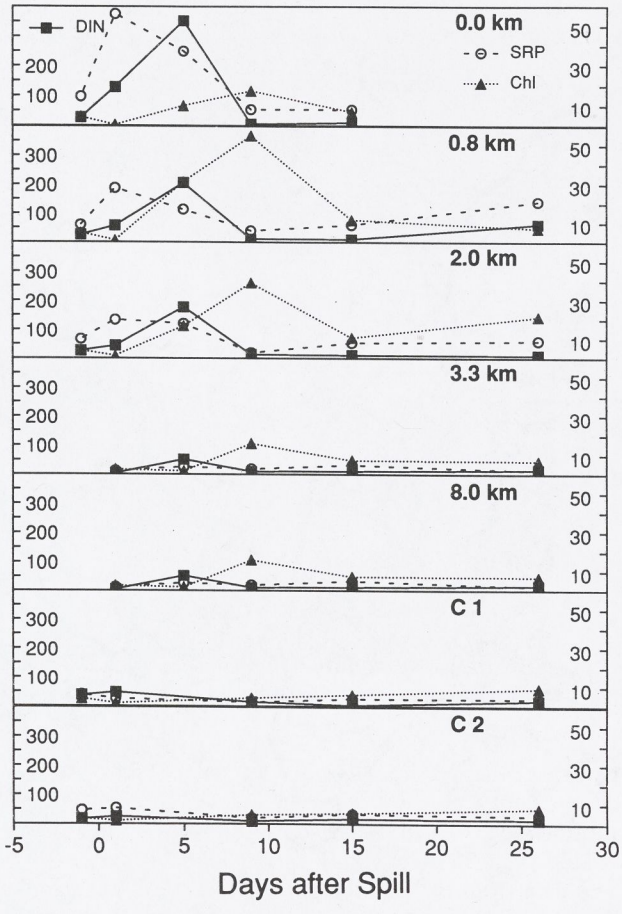


Zooplankton was collected by filtering 10 L of bioassay water through the 63-μm mesh bucket of the previously mentioned Schindler trap. Primary production measurements were made immediately after the experiment was terminated.

Analyses

Ammonia was analyzed using the phenolhypochlorite method (Solórzano 1969); nitrate, plus nitrite, was analyzed using a diazotization-coupling reaction (Strickland and Parsons 1972). DIN is reported as the sum of ammonium, nitrate, and nitrite and may include methylamine compounds from the breakdown of MITC (del Rosario et al. 1994). SRP was determined by the phosphomolybdate method (APHA 1976). We calculated standard curves (0, 5, 10, 25, 50, 100 μg/L) for ammonium, nitrate, and soluble reactive phosphorus on each sampling date. Standard curves were carried out in duplicate, as were lake measurements for ammonium and nitrate. The average coefficient of variation for these duplicate measurements was 2.3 ± 3.7% and 2.2 ± 3.1% for ammonium and nitrate, respectively. Water samples for analyses of DIN and SRP were filtered through GF/C filters prior to analysis. Chlorophyll *a* concentrations were determined using the fluorometric method with acid correction for phaeophytin (Strickland and Parsons 1972) after freezing for 48 h and extracting with methanol in the dark at 4°C for 24 h (Marker et al. 1980). Primary production, ^{14}C uptake, in the bioassay experiment was determined by placing 250-mL water samples in clear glass bottles inoculated with 185 kBq $H^{14}CO_3$, with one dark bottle included for each treatment. Bottles were suspended at 5 m depth for approximately 4 h after which their contents were filtered through 0.4-μm Millipore filters. The filters were placed in a thin window gas flow, Geiger-Müller

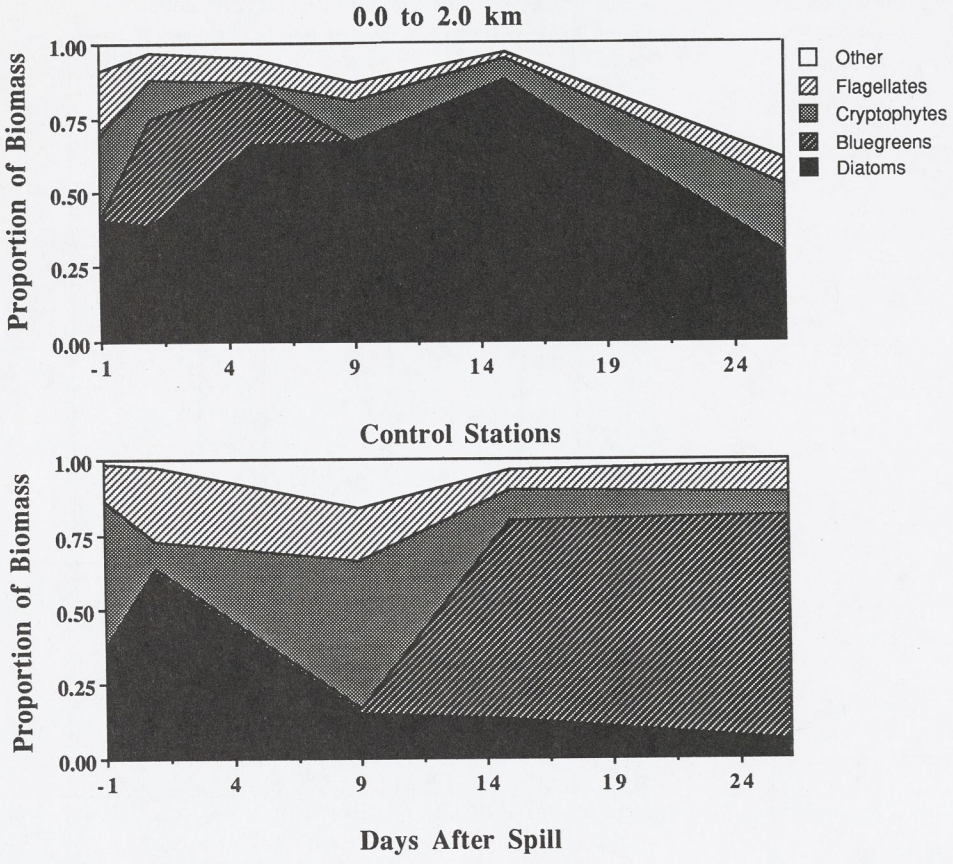
Fig. 3. Dissolved inorganic nitrogen (DIN), soluble reactive phosphorus (SRP), and chlorophyll *a* (Chl) concentrations (μg/L) through time for the impacted stations 0.0 km through 8.0 km and the control stations C1 and C2.



proportional counter to determine ^{14}C uptake, after subtraction for dark uptake. Dissolved inorganic carbon concentration was determined by infrared gas analysis (Roberts and Smith 1988). MITC analyses for our bioassay samples were carried out by American Environmental Laboratories Corporation under the direction of the California Department of Fish and Game using U.S. EPA Method 131. This is the same method used to determine the MITC concentrations reported by CRWQCB (1991).

Zooplankton community composition and biomass was determined by identifying individuals to genera or species using a dissecting (crustaceans) or an inverted compound (rotifers) microscope. The entire sample was counted for crustacean enumeration, while a subsample with >400 individuals was counted for the rotifers. Average crustacean species biomass was estimated by measuring the length of 20–30 individuals and converting to biomass using standard taxa length to weight regressions (McCaully 1984). Rotifer species biomass values were taken from the literature (Makarewicz and Likens 1979). Algal biovolume was determined by calculating cells per millilitre for each species using an inverted light microscope and the Utermöhl technique, and converting to biovolume using previously

Fig. 4. Average phytoplankton community composition for the 0.0, 0.8, and 2.0 impacted stations (upper panel) as well as the two control stations (lower panel) through time.



determined algal species specific biovolume values (Elser and Goldman 1991; D. Hunter, unpublished data).

The data from the dilution experiment were statistically analyzed with a single-factor ANOVA, using untransformed data for DIN and SRP and log-transformed data for chlorophyll concentrations and zooplankton biomass. One replicate of the 13.5% treatment was excluded from the statistical analysis and corresponding figures as it was an extreme outlier for all the parameters measured. Relative treatment responses for Chl concentrations and primary production in the dilution experiment were compared using two-tailed *t*-tests.

Results

Inorganic nutrients

DIN (ammonium, nitrate, and nitrite) concentrations increased immediately after the spill and peaked at 200–350 μg/L at 0.0–2.0 km, respectively, on day 5 (Fig. 3). These concentrations then returned to their initial low values as an algal bloom, see below, peaked on day 9. The increase in DIN concentrations was strongly related to distance from the Sacramento River inflow with levels declining with distance from the inflow. Similar to DIN, SRP increased markedly after the spill (Fig. 3). The peak values observed were 55–30 μg/L at 0.0–0.8 km, respectively, on day 1. Like DIN, SRP concentrations returned to their previously low levels as the algal bloom peaked. Unlike DIN, SRP concentrations decreased sooner after the spill and high concentrations were not observed as far into the reservoir (Fig. 3).

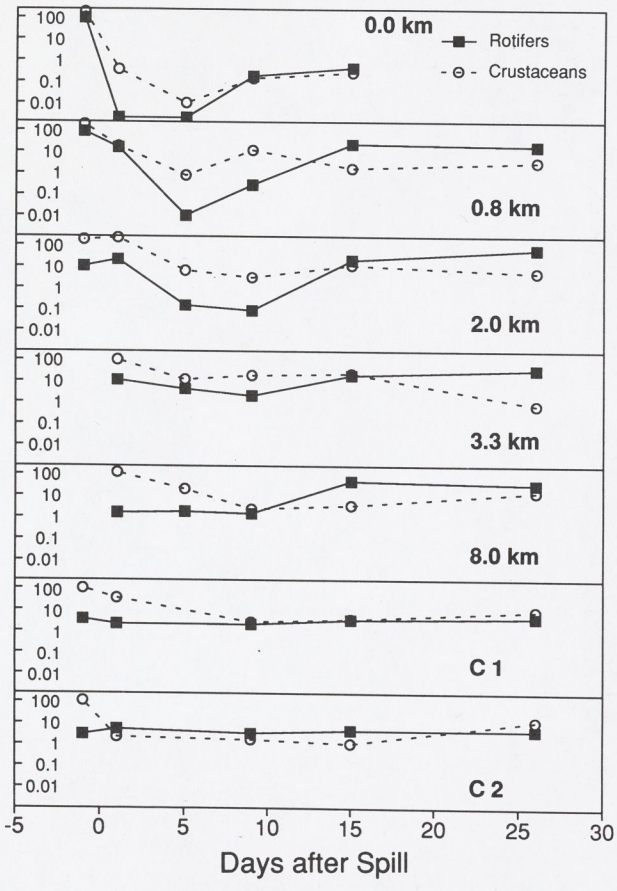
Chlorophyll *a*

Chlorophyll concentrations decreased immediately after the spill entered Shasta Lake, but then rebounded dramatically by days 5 and 9 as an algal bloom developed (Fig. 3). This bloom was dominated by diatoms, 74% of biomass at stations 0.0–3.3 km, particularly *Nitzschia palea*, *Cyclotella atomus*, and *Synedra ulna*. However, other algal groups were also common (Brett et al. 1992). This bloom clearly extended to 3.3 km, and may have also been present 8.0 km into the reservoir (Fig. 5). Figure 6 shows the phytoplankton community composition for the 0.0- to 2.0-km impacted and control stations during this investigation. These data show the strong dominance by diatoms at the impact stations after the spill and dominance by cyanobacteria at the control stations during this same time.

Zooplankton

Of the measured parameters, zooplankton had the most severe response to the spill entering the reservoir. At 0.0 km, there was a 50 000 fold decrease in rotifer abundance from day −1 to day 1. Rotifer abundance decreased from 862 *Polyarthra vulgaris*/L, 262 *Keratella cochlearis*/L, and 208 *Synchaeta* spp./L on day −1 to only 1 potentially intact *K. cochlearis* individual in an entire 50-L sample

Fig. 5. Rotifer and crustacean biomass (μg dry weight/L) through time for the impacted stations 0.0 km through 8.0 km and the control stations C1 and C2.

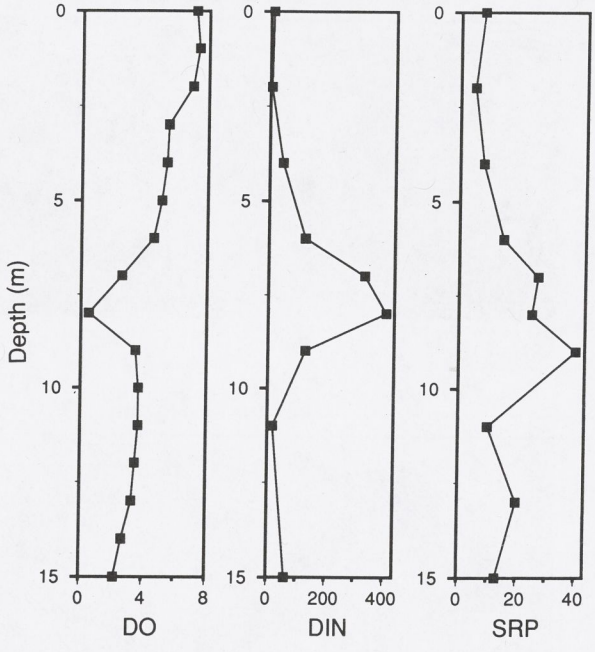


on day 1. Overall the depression in rotifer biomass was very extreme from 0.0 to 2.0 km into Shasta Lake (Fig. 5). However, rotifers recovered to approximately 30% of their initial numbers at 0.8 and 2.0 km by day 15. There was little variation in rotifer biomass at the control stations during the course of our observations. The crustacean zooplankton also showed a dramatic negative response to the spill (Fig. 5). Unlike the rotifers, there was only a weak trend towards recovery of the crustacean zooplankton by day 26 at 0.0 to 2.0 km. Also unlike the rotifers, there was considerable variability in crustacean zooplankton biomass at the control stations, particularly between days −1 and 1. Some of this variability may have been due to the fact that we sampled station C 1 at sunset and station C 2 at approximately 1 h after sunset on day −1. All subsequent samples were collected during full sunlight. Crustacean zooplankton typically undergo pronounced diurnal vertical migrations, and it is not unusual to observe many more crustacean zooplankters in surface waters at night than during the day (Lampert 1989).

Dissolved oxygen and nutrient profiles

Five days after the spill entered Shasta Lake a pronounced DO minimum of 0.5 ppm was first noticed at 8 m at 3.3 km. Associated with this mid-depth DO minimum were

Fig. 6. Dissolved oxygen (DO; mg/L), dissolved inorganic nitrogen (DIN; μg/L), and soluble reactive phosphorus (SRP; μg/L) profiles for station 3.3 km on day 5.

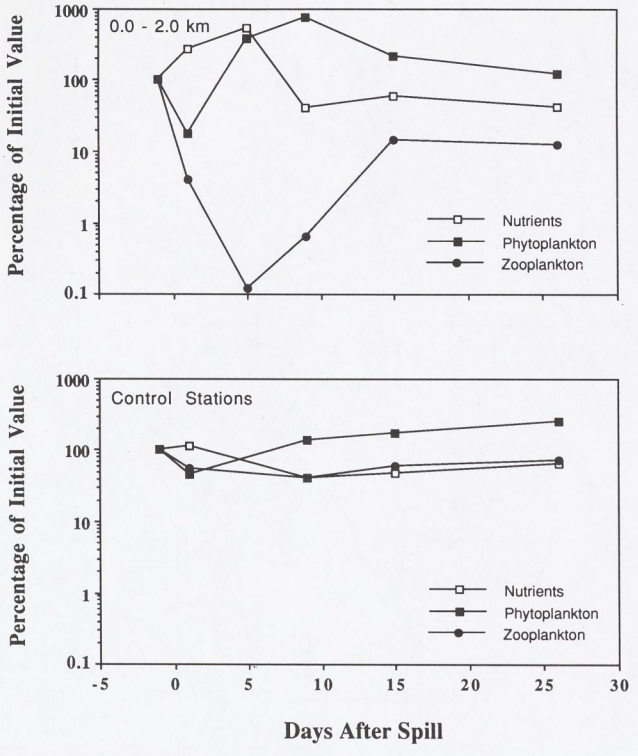


equally prominent DIN and SRP maxima (Fig. 6). The DIN maximum was composed almost exclusively of ammonium (Brett et al. 1992). The DO profile shown in Fig. 6 is representative of DO profiles seen at stations 3.7, 4.1, and 4.5 km which all had pronounced DO minima averaging 1.2 ± 0.6 ppm at 8–9 m depth. There was also a weaker DO discontinuity seen at stations 6.5 and 8.0 km on Day 5. Thereafter, the lake DO profiles in the vicinity of the river inflow showed the effects of the subsequent algal bloom, with very high DO concentrations at the surface and abruptly diminishing values with depth (Brett et al. 1992). As the algal bloom receded, the DO profile returned to patterns seen before the spill and at the control stations (Brett et al. 1992).

Generalized field results

To allow the major parameters to be viewed simultaneously we have calculated a generalized response to the spill for the 0.0, 0.8, and 2.0 km stations and compared these results with those for the two control stations (Fig. 7). These values were obtained by first calculating the geometric mean for DIN, SRP, and Chl concentrations, as well as rotifer and crustacean biomass for the 0.0–2.0 km and the control stations for each sampling date. These geometric mean values were then converted back to arithmetic numbers, and divided by the initial (day −1) mean for the respective impact or control stations. For the sake of simplicity, we have only plotted the average of the DIN and SRP as well as the average rotifer and crustacean biomass responses. These results show that nutrient concentrations increased immediately after the spill, and then returned to approximately initial values as an algal bloom developed. The chlorophyll results show an immediate crash of the phytoplankton and a subsequent and equally dramatic algal

Fig. 7. Generalized response of nutrient and chlorophyll concentrations and zooplankton biomass of the impacted 0.0, 0.8 and 2.0 km stations (upper panel) and the control stations (lower panel).



bloom. The zooplankton crashed to very low levels by day 5 and then began to recover. There was only moderate change in nutrient and chlorophyll concentrations and zooplankton biomass at the control stations during this time.

Dilution bioassay

The results of the dilution bioassay can be compared with those seen in the reservoir at day 9 when an algal bloom had peaked, dissolved inorganic nutrients were exhausted and zooplankton biomass was still severely depressed. The bioassay MITC arithmetic mean concentrations measured on day 5 were: control (0.0 μg/L), 1% (0.8 ± 0.6 μg/L), 3.5% (4.3 ± 0.3 μg/L), 13.5% (15.5 ± 0.5 μg/L), and 50% (41.0 ± 0.7 μg/L). The measured MITC concentrations on day 8 were: control (0.0 μg/L), 1% (0.3 ± 0.6 μg/L), 3.5% (3.5 ± 0.1 μg/L), 13.5% (14 ± 0 μg/L), and 50% (26.0 ± 2.2 μg/L) (also see Table 1). Values below the limit of detection (1.1 μg/L) were assumed to be 0.0 μg/L when calculating treatment means. There was a strong concordance between our dilution levels and measured MITC concentrations across all treatments, with very little variability within treatments.

Similar to the results seen in Shasta Lake on day 9, the dilution bioassay showed relatively low DIN and SRP concentrations, a dramatic stimulation of chlorophyll concentrations, and a pronounced depression of zooplankton biomass (rotifers plus crustaceans) in the high contamination treatments (Fig. 8, Table 1). The phytoplankton biomass in the 50% contamination treatment was strongly

Table 1. Single-factor ANOVA results for MITC concentrations and biological responses for the dilution bioassay experiment.

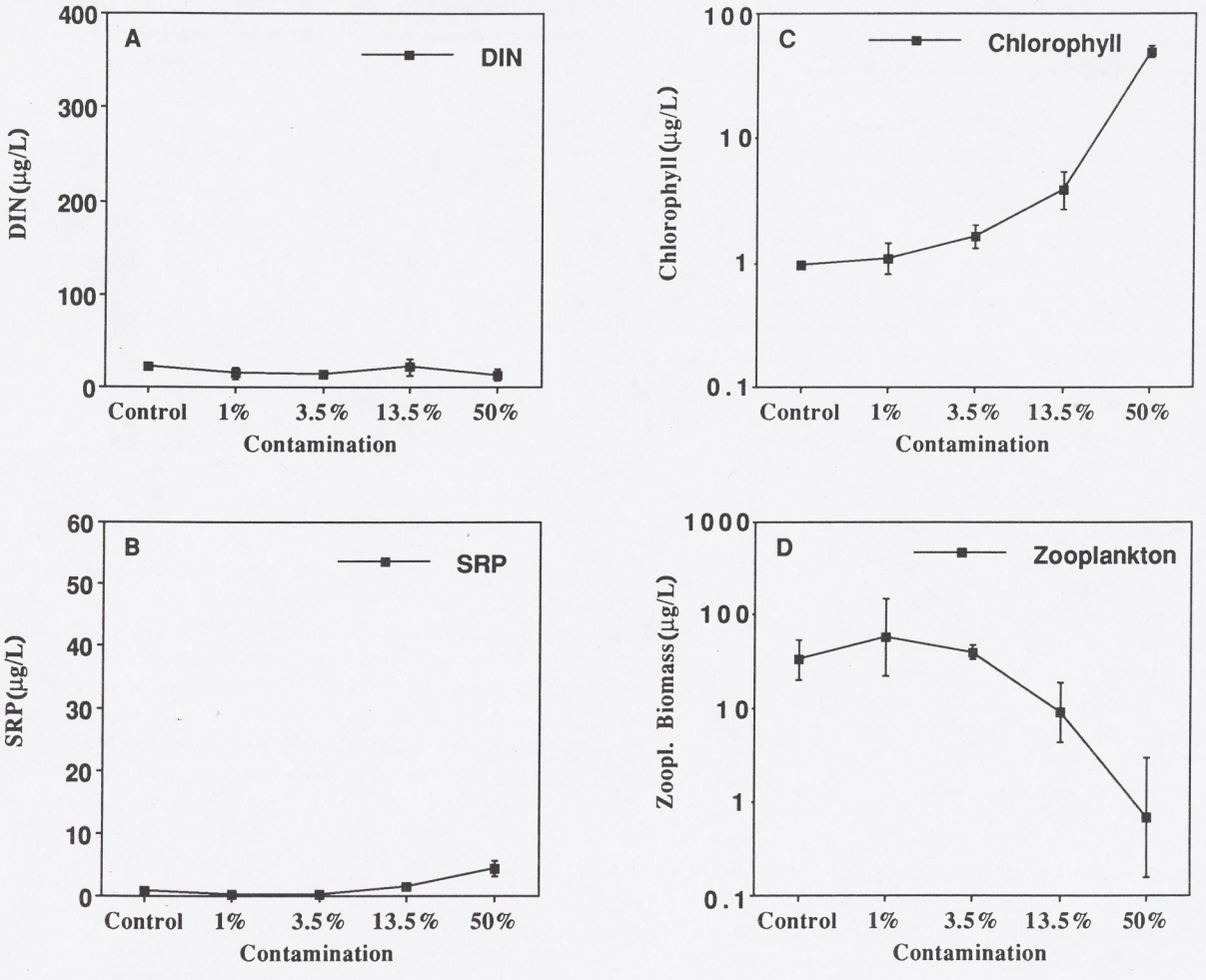
Parameter	df	MS	*F*	*P*
MITC day 4				
Contamination	4	1180	4232.25	0.0001
Error	14	0.279		
MITC day 8				
Contamination	4	394	264.09	0.0001
Error	10*	1.49		
DIN				
Contamination	4	67.0	2.15	0.1279
Error	14	31.1		
SRP				
Contamination	4	11.9	34.52	0.0001
Error	14	0.508		
Chlorophyll				
Contamination	4	1.98	225.33	0.0001
Error	14	0.0088		
Zooplankton				
Contamination	4	2.46	16.30	0.0001
Error	14	0.151		

*4 samples lost due to missing labels.

dominated (average 92% of biomass) by an unidentified small green coccoid alga and the diatom *Nitzschia palea* (Brett et al. 1992). A comparison of spill-driven stimulation of chlorophyll concentrations and spill-driven stimulation of primary production, relative to the control treatment mean, shows primary production was stimulated to a much greater extent than were chlorophyll concentrations at all contamination levels (paired *t*-test, $P < 0.0001$) (Fig. 9).

Although initial MITC concentrations were not measured in the bioassay experiment these were roughly estimated by assuming a first-order loss, the most appropriate model to describe loss of pesticides from water (Tinsley 1979), and back-calculating using known MITC concentrations from experiment days 5 and 8. Using the 11 cases where MITC concentrations above the detection limit were recorded on both experiment day 5 and 8, we calculated initial MITC concentrations (y) in micrograms per litre were equal to 177 times the dilution level (x); $y = 177x$, $R^2 = 0.99$. A zooplankton biomass 8-d LC_{50} was then calculated by fitting a second-order polynomial regression to the log-transformed zooplankton biomass and initial MITC concentration estimates from the experiment ($R^2 = 0.83$) and calculating the contamination level at which treatment biomass would equal 50% of control biomass. These calculations gave a zooplankton biomass 8-d LC_{50} of 15 μg/L MITC. The MITC concentration at which algal biomass was doubled was calculated by fitting a second-order polynomial regression to $\log_{10}$-transformed Chl and MITC concentration data ($R^2 = 0.98$). This value was 9 μg/L MITC. In a similar fashion, the contamination level at which primary production was doubled was found to be 1 μg/L. Because we were forced to estimate initial MITC concentrations these values should be interpreted with caution.

Fig. 8. Response of DIN (A), SRP (B), chlorophyll (C) and zooplankton biomass (D) to the various contamination levels in the dilution bioassay experiment. The values plotted are mean ± 1 SD.



Discussion

We demonstrated that the 1991 Vapam® spill at the Cantara Loop on the upper Sacramento River caused a major perturbation of the planktonic ecosystem of the Sacramento Arm of Shasta Lake. Of the parameters measured the zooplankton showed the most severe response with only 1 in 50 000 rotifers surviving at the 0.0 km station one day after the spill entered Shasta Lake. The response of the crustacean zooplankton was nearly as dramatic. Calculations from the dilution bioassay experiment gave a zooplankton biomass 8-d LC_{50} of 15 µg/L MITC, indicating this compound is extremely toxic to zooplankton. The initial drop in chlorophyll concentrations after the spill entered the reservoir was much less severe than that seen for the zooplankton. In fact, the most prominent feature of the phytoplankton response to the spill was a pronounced diatom bloom which peaked after 9-d. This algal bloom was probably driven by the very high inorganic nutrient concentrations in the reservoir immediately after the spill and by the almost total absence of zooplankton grazers for the majority of the bloom period, both of which are indirect effects of the spill from the perspective of the algae. The dilution bioassay experiment suggests that the spill had a greater effect on Shasta Lake's primary production than increases in lake chlorophyll concentration would otherwise indicate. There was a huge pulse of inorganic nitrogen and phosphorus associated with the spill. Inorganic nutrient concentrations returned to prespill levels as the algal bloom peaked. This spill also caused a pronounced mid-depth DO depression from 3.3 to 4.5 km from the river inflow on day 5.

Single species biotoxicity tests using fathead minnows, *Pimephales promelas*, the cladoceran *Ceriodaphnia dubia*, and the alga *Selenastrum capriconutum* were conducted soon after the spill occurred (California Department of Fish and Game, unpublished data). These biotoxicity assays showed MITC to be toxic, 50% mortality, at 110, 100, and 74 µg/L, respectively. If one were to have used these values and lake MITC concentrations (Fig. 2) to predict an expected effect of the spill on Shasta Lake, strong effects would only have been expected within 1 km of the river inflow with recovery possible after only 48 h. Instead, the spill affected a much larger area of the reservoir over a period of several weeks. Our field and dilution bioassay results indicate that MITC is far more toxic to zooplankton

than the single species test with *Ceriodaphnia* suggested. Although the single species tests with *Selenastrum* did predict a toxic effect of the spill on the phytoplankton, and this was confirmed in the field observations of reduced chlorophyll concentrations, the most pronounced algal response to the spill, i.e., the bloom, was unexpected from these test results and an indirect effect of the spill. Furthermore, the single species tests suggested algae might be more sensitive to MITC than zooplankton, while our field observations and dilution experiment clearly showed the zooplankton were much more sensitive to MITC toxicity.

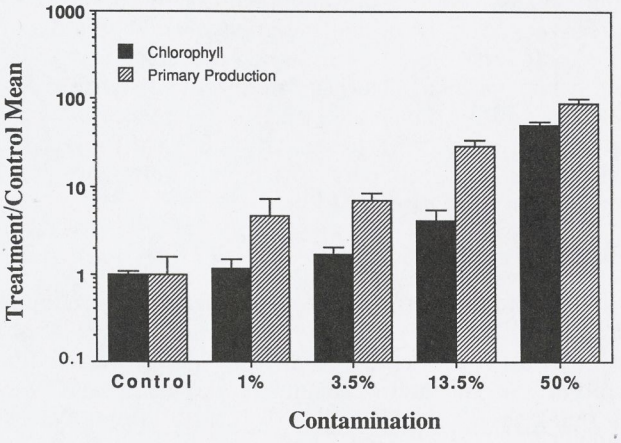
Unlike the single species biotoxicity tests, the dilution experiment confirmed the major findings of our field investigation on day 9. High contamination levels resulted in massive zooplankton mortality and a dramatic algal bloom. The algal bloom was probably caused by the very high nutrient concentration originally present in the contaminated lake water (see DIN and SRP concentrations at station 0.0 km on day 1; Figs. 3 and 4), and greatly reduced zooplankton grazing. The dilution experiment also showed that the level of contamination, analogous to distance from the river inflow (Fig. 2), was clearly related to the strength of the biological response seen.

Our results show that in some cases the indirect effects of the spill were as large or greater than the direct impacts of the spill. This was true for the huge pulse of inorganic nutrients that probably originated from decaying plant and animal matter in the upper Sacramento River and Shasta Lake. This is also true for the algae that responded to the spill with a bloom that was both more pronounced than the initial MITC-induced mortality and much longer lasting. In contrast, the zooplankton mainly showed a direct response to the spill.

The speed at which organisms recover after disturbances is related to characteristics of the organism (dependent factors) and characteristics of the perturbed environment (independent factors) (Niemi et al. 1990). Dependent factors include an organism's generation time and reproductive characteristics (which act to determine the population's intrinsic rate of increase), presence of resistant or resting stages, propensity to disperse, and predation and competitive interactions with other species. Independent factors included changes in the physical habitat, residual toxicity, time of impact, and presence of refugia (Niemi et al. 1990). In Shasta Lake, many of these factors acted in concert to explain the rapid recovery of the phytoplankton to the initial spill-induced mortality. These included the very high intrinsic rates of population increase characteristic for almost all algae (i.e., population doubling times are usually on the order of 1 d or less at temperatures between 20 and 30°C), incomplete mortality (i.e., approximately 10–30% of the algae actually survived the spill as indicated by chlorophyll concentrations), a total absence of predation for several weeks after the spill, and rapid dissipation of the MITC. In addition, the spill occurred in the middle of the plankton growing season when Shasta Lake was warm and the days were long, and inorganic nutrient concentrations were very high in the vicinity of the spill.

Many of these factors also acted to explain the fairly rapid recovery of the rotifer zooplankton. These included the relatively high innate capacity for population increase (population doubling times are generally on the order of

Fig. 9. Relative responses of chlorophyll concentration and primary production to each contamination level treatment in the dilution experiment. These values (mean ± 1 SD) were generated by dividing each replicate of each treatment by the mean of the control treatment.



1 week or less at ambient temperatures), the production of resistant resting eggs by rotifers (i.e., a "rotifer egg bank" would have existed before the spill occurred), greatly reduced competition with and predation from crustacean zooplankters, abundant food, rapid dissipation of the MITC, and the fact that the spill occurred during the summer growing season. The rotifers recovered more slowly than the algae because they require more time to achieve a population doubling and, probably most importantly, because the rotifers were much more sensitive to the residual MITC still present in Shasta Lake until approximately 10 d after the spill. It should be noted that the remaining resistant species of algae showed tremendous growth at MITC concentrations approximately twice the estimated LC_{50} for zooplankton biomass in the dilution experiment.

Unlike the rotifers the crustacean zooplankton showed only weak trends towards recovery by day 26. This delayed recovery of the crustacean zooplankton is somewhat surprising because most of the dependent and independent factors mentioned above for the rotifers also apply to crustacean zooplankters. The only substantial difference between these factors for the crustacean and rotifer zooplankton is that cladocerans should require slightly more time to achieve a population doubling than rotifers. Copepods, which reproduce sexually as opposed to the parthenogenic reproduction of cladocerans and rotifers, could require substantially more time to achieve a population doubling than either cladocerans or rotifers. However, the initial crustacean zooplankton assemblage at the impacted stations was dominated by cladoceran zooplankters, 74–95% *Daphnia* and *Bosmina* by biomass, which given favorable conditions can achieve very high population growth rates. Furthermore, a literature review by Niemi et al. (1990) found rotifers and cladocerans usually required the same period of time to recover after disturbances.

Conclusions

A spill of metam sodium caused a huge mortality of rotifer and crustacean zooplankton, a large mortality of phytoplankton

and a subsequent bloom, and a large pulse of dissolved inorganic nitrogen and phosphorus in Shasta Lake, California. The phytoplankton exceeded initial biomasses within 5 d of the spill entering Shasta Lake, the nutrients returned to approximately prespill levels after 9 d (when the algal bloom peaked), the rotifer zooplankton showed substantial recovery after 15 d, and the crustacean zooplankton showed only weak signs of recovery 26 d after the spill. The effect of the spill was clearly related to the distance from of the river inflow, moderate effects seen at a 3.3 km station, and only weak effects seen at an 8.0 km station. In several cases indirect impacts of the spill were more pronounced than were direct effects.

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SPECIES-DEPENDENT EFFECTS OF ZOOPLANKTON ON PLANKTONIC ECOSYSTEM PROCESSES IN CASTLE LAKE, CALIFORNIA[1]

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Abstract. Freshwater zooplankton communities typically undergo pronounced seasonal succession and often show dramatic responses to external factors such as changes in zooplanktivore abundance. For this reason it is important to assess how common zooplankton species differ in their grazing impacts on planktonic ecosystems. To accomplish this we used single-species treatments with *Diacyclops bicuspidatus thomasi, Daphnia rosea, Diaptomus novamexicanus,* and *Holopedium gibberum* in situ in Castle Lake, California. These taxonomically diverse zooplankters differ markedly in feeding modes and typical seasonal population dynamics. We measured the response of nutrient concentrations, bacterioplankton abundance, phytoplankton species composition and biomass, primary production, a grazing index (phaeophytin/chlorophyll *a*), and microzooplankton to our single-species treatments.

The filter-feeding cladocerans *Daphnia* and *Holopedium* and the raptorial filter-feeding calanoid copepod *Diaptomus* showed several effects typical of herbivorous zooplankton. These included increasing dissolved nutrient concentrations, decreasing algal biomass and the abundance of several common algae, increasing a grazing index, increasing the ratio of bacterial to algal biomass, as well as depressing ciliate microzooplankton abundance. The raptorial cyclopoid copepod *Diacyclops* was apparently exclusively predaceous as it decimated the ciliate and rotifer microzooplankton, but had no notable effect on the other measured parameters relative to zooplankton-free controls. *Diacyclops* had the greatest effect on the microzooplankton and *Daphnia* and *Diaptomus* had the greatest effect on inorganic nutrients and characteristics of the phytoplankton. *Holopedium* had qualitatively similar but weaker impacts compared to *Daphnia* and *Diaptomus*. None of the zooplankton treatments had an effect on bacterioplankton abundance, nor did grazing by any of these zooplankters increase total algal primary production. Our results suggest differences in the grazing effects of common freshwater zooplankton can be pronounced and indicate that both seasonal succession and long-term shifts in the zooplankton community structure should have marked effects on microzooplankton competitors and prey, the phytoplankton, and nutrient cycling.

Key words: *Castle Lake;* Daphnia; Diacyclops; Diaptomus; *grazing impacts;* Holopedium; *planktonic ecosystem; zooplankton.*

Introduction

Herbivores can influence the structure and dynamics of plant communities by preferentially removing specific plants or parts of plants, by regenerating nutrients, and by competitively suppressing other herbivores. These direct effects can in turn result in a myriad of indirect effects, which can dramatically alter the structure and dynamics of ecosystems, often in unforeseen ways (Paine 1992). Most investigations of grazing effects on plant communities have used enclosure/exclosure designs with a dominant herbivore or all herbivores. These studies are able to determine the influence of herbivores on plant communities, and in ecosystems where there are only one or a few main herbivores this may be sufficient. However, many herbivore communities are extremely dynamic, with the species composition of the community shifting mark-

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edly both seasonally and long term. This is particularly true of freshwater zooplankton communities. In cases where the herbivore community is dynamic, it is imperative to gain insights into how different herbivores impact plant communities.

Research actually assessing species-specific grazing impacts has generally examined aquatic systems and has concentrated on a few ecosystem types (e.g., rocky intertidal zones, coral reefs, and streams). The behavior and impact of different herbivores varies markedly from system to system. Terrestrial research has shown grazers often attack different parts of plants or attack the same plants at different times of the year (e.g., Karban and Strauss 1993); further, it is widely known that phytophagous insects often attack only one host plant species when many potential host species are available. Working in the marine intertidal zone, Fletcher (1987) and Paine (1992) found some grazers had very strong negative impacts on algal biomass or recruitment, while other grazers had no impact or a positive impact on the algae. Research on Caribbean coral communities showed urchins have a much greater impact on attached algae than do herbivorous fishes (e.g., Morrison 1988). Studies on stream insects have shown pronounced differences between species in grazing impacts on periphytic algal communities. In some cases different insect species completely changed the periphyton species composition or dramatically altered the pattern of algal distribution (e.g., DeNicola et al. 1990, Feminella and Resh 1991).

While some research on zooplankton has specifically examined species-specific effects on the phytoplankton (Knisely and Geller 1986), most studies have used treatments with or without zooplankton (Lehman and Sandgren 1985, Bergquist and Carpenter 1986) or contrasted large-size vs. small-size dominated zooplankton communities (Vanni 1987, Cyr and Pace 1993). With the exception of Knisely and Geller (1986), these studies do not indicate how zooplankton species shifts drive changes in the planktonic ecosystem.

Much of the past research on species differences in grazing effects, particularly the stream research, has emphasized the importance of feeding behavior and morphology in ultimately explaining subsequent interspecies differences. The taxonomically diverse zooplankters examined in the present investigation represent a broad range of feeding strategies, from the raptorial cyclopoid copepod *Diacyclops,* to the raptorial and filtering calanoid copepod *Diaptomus* and the exclusively filter-feeding cladocerans *Daphnia* and *Holopedium.* DeMott (1986) and DeMott and Moxter (1991) demonstrated that zooplankton have varying abilities to discriminate between potential food particles of similar morphology based on taste. Rotifers were found to be the most selective followed by copepods, while cladocerans (and particularly *Daphnia*) usually fed nonselectively. Hessen (1985) concluded that the ability to retain small particles was strongly correlated with filtering comb morphology, with zooplankters having fine combs selecting the smallest particles. Simply based on feeding strategy, one could predict that these zooplankters would have markedly different effects on the species composition of the algae, rates of phytoplankton primary production, nutrient regeneration, competitors, etc. Crustacean zooplankton species are also known to differ dramatically in behavior, life history characteristics, growth response to resources, susceptibility to algal toxins and elemental composition (Lynch 1980, Lampert and Muck 1985, Stich 1989, Andersen and Hessen 1991, Lundstedt and Brett 1991). Thus one can predict a priori that different zooplankton species will have distinct effects on the entire planktonic ecosystem.

To contribute to the understanding of zooplankton species impacts on planktonic ecosystems, we used *Diacyclops bicuspidatus thomasi, Daphnia rosea, Diaptomus novamexicanus,* and *Holopedium gibberum,* the four most common crustacean zooplankton in Castle Lake, California. The zooplankton community of Castle Lake is very dynamic seasonally in terms of total community biomass and species contributions to biomass. Further, the zooplankton community of Castle Lake has recently shifted structure in response to fish community manipulations, which resulted in increased zooplanktivory due to increased abundance of golden shiners (*Notemigonus crysoleucas*). During our whole-lake manipulation, the zooplankton community shifted from biomass dominance by *Daphnia* and *Diaptomus,* and seasonally *Holopedium,* to dramatically increased representation of *Diacyclops* and decreased representation by *Daphnia* and *Diaptomus.* During the time that the fish community was manipulated and the zooplankton community structure changed, water transparency declined and phytoplankton primary production increased (J. J. Elser, *personal observation*).

The grazing response variables examined in the present study were dissolved inorganic nitrogen (DIN), soluble reactive phosphorus (SRP), the ratio of DIN/SRP, bacteria cell abundance, bacteria biovolume per algal biovolume, algal community structure and biovolume, phaeophytin per chlorophyll *a,* ^{14}C uptake, ^{14}C uptake per unit algal carbon, and ciliate and rotifer abundance. DIN and SRP are measures of zooplankton nutrient regeneration, the ratio of DIN to SRP is a measure of the nature of nutrient cycling and may determine the direction of algal succession (Sterner et al. 1992), the ratio of phaeophytin (a chlorophyll breakdown product) to chlorophyll *a* is an index of grazing (Carpenter and Bergquist 1985), ^{14}C uptake is a measure of total primary production, and ^{14}C uptake per unit algal carbon is a measure of relative primary production.

Methods

To test the differential grazing effects of the four most common zooplankters in Castle Lake on microzooplankton competitors, the phytoplankton, primary

production, the bacterioplankton, and nutrient cycling, we removed all larger zooplankton from lake water using a screen and created individual species treatments by adding a previously determined number of individuals to each experimental vessel. Differences between each zooplankton species treatment and a zooplankton-free control treatment were considered either direct or indirect effects of the zooplankton species tested. The length of the experiment, 8 d, was sufficient to allow trends to develop for the microzooplankton, which have generation times of a few days to a week, but short enough to still detect trends among short-term processes such as nutrient regeneration.

Lake water was collected at 1, 3, and 5 m depth and passed through a 83-μm mesh screen to remove large zooplankton. Twenty-five 10-L cubitainers were incrementally filled with this screened lake water. The individual zooplankton species treatments were created by adding $\approx$15 *Diacyclops,* 15 *Daphnia,* 15 *Diaptomus,* or 3 *Holopedium*/L to each of five separate cubitainers. We used individual zooplankter abundances in our species treatments, which were similar to high abundances seen for those species in Castle Lake. This was done in order to provide sufficiently high treatment abundances to detect a treatment effect and to assure that our results were still biologically meaningful. The experiments were started with mainly adult or late-stage juvenile zooplankters, but by the end of the experiment all treatments were dominated (in terms of biomass) by juveniles of the treatment species. The adult individuals used to start the experiment had mean dry masses of 2.6, 3.6, 8.0, and 15.4 μg/individual for *Diacyclops, Diaptomus, Daphnia,* and *Holopedium,* respectively. The removal (control) treatment consisted of screened lake water added to five cubitainers.

The cubitainers were incubated at 5 m depth in Castle Lake. The experiment was started on 13 June 1991 and ended 8 d later on 21 June 1991. The temperature at 5 m depth was 13° and 15°C at the beginning and end of the experiment, respectively. The seasonal average for light penetration at 5 m is 23 $\pm$ 4.6% ($\pm$ 1 SD) of surface values. For a more detailed description of Castle Lake, see Goldman and de Amezaga (1984).

At the end of the experiment, samples for crustacean zooplankton enumeration were taken by pouring 6 L of each treatment replicate through a 83-μm mesh screen and preserving with a Lugol's and sucrose solution. One litre of unfiltered water preserved with Lugol's was collected for ciliate, rotifer, and nauplii enumeration; 125 mL of sample water, also preserved with Lugol's, was collected for phytoplankton species identification and enumeration. Ten millilitres of sample water were preserved with 2% formalin for bacteria cell counts. One litre of unpreserved sample water was collected for analyses of nitrate, ammonia, SRP, chlorophyll *a,* phaeophytin, and ^{14}C incorporation. Water intended for nutrient and pigment analyses was screened through a 83-μm mesh within 1 h after collection to remove large zooplankton.

Zooplankton juveniles and adults were enumerated and their biomass calculated using previously determined dry masses for these size classes of Castle Lake zooplankton (Redfield 1979). The rate of zooplankton biomass change for the treatment zooplankters was calculated according to the logistic growth equation using the initial and final treatment zooplankter biomass and an 8-d sampling interval. Ciliates were counted by concentrating the 1 L of Lugol's preserved sample to a small volume by sedimentation for 3 d and counting under an inverted light microscope using the Utermöhl technique. For the removal, *Daphnia, Diaptomus,* and *Holopedium* treatments, 500 mL of the sample was counted, while the entire sample was counted for the *Diacyclops* treatment. These samples were counted within 4 mo of collection and were stored at room temperature until enumeration. Algae were also enumerated using the Utermöhl technique. Algal biovolume was estimated from cell abundances and species cell biovolume values for Castle Lake and Lake Tahoe algae (Elser and Goldman 1991; D. Hunter, *unpublished data*). Epifluorescence microscopy of acridine-orange stained and formalin-fixed samples was used to count bacteria (Hobbie et al. 1977). Sterile water was used to prepare the stain, and blanks were run for each counting session.

Ammonia was quantified using the phenolhypochlorite method (Solórzano 1969). Nitrate, plus nitrite, was analyzed using a diazotization-coupling reaction (Strickland and Parsons 1972). SRP was measured by the phosphomolybdate method (American Public Health Association 1976). Chlorophyll *a* and phaeophytin concentrations were determined using the fluorometric method with acid correction for degradation products (Strickland and Parsons 1972) after freezing for 48 h and extracting with methanol in the dark at 4°C for 24 h (Marker et al. 1980). Primary production determinations were made at the end of the experiment, with one light bottle for each replicate of each treatment and one composite dark bottle for each treatment. This was done by placing 250-mL water samples in clear glass bottles inoculated with 185 kBq (5 μCi) $H^{14}CO_3$. Bottles were suspended at 5 m depth for $\approx$4 h, after which their contents were filtered onto 0.4-μm Millipore filters. The filters were placed in a gas proportional detector to measure ^{14}C. Dissolved inorganic carbon concentration was determined by infrared analysis of subsamples placed in evacuated blood-collection tubes and preserved with chloroform (Roberts and Smith 1988).

Data Analyses

Since we had a possible covariation between our zooplankton species treatments and the zooplankton biomasses of these treatments, i.e., there were systematic differences in the zooplankton biomass between

TABLE 1. Crustacean zooplankton abundance, dry biomass, and fecundity in the removal and zooplankton treatments. Initial and final observations are given, values presented are mean ± 1 SD. Abundance estimates do not include nauplii.

Treatment	Initial individuals (ind./L)	Initial biomass (μg/L)	Initial percent nauplii	Initial fecundity (eggs/♀♀)*	Final individuals ind./L	Final biomass (μg/L)	Final percent nauplii	Final fecundity (eggs/♀♀)*	Rate of biomass change per day
Removal	...	3.8	100	...	...	8.5 ± 3.2	97 ± 4	...	0.095 ± 0.045
Diacyclops	13.7	33	11	11	7.6 ± 1.3	58 ± 9.6	70 ± 11	1.8 ± 0.49	0.067 ± 0.023
Daphnia	15.2	120	3	2.0	33.8 ± 6.2	175 ± 33	5 ± 3	0.30 ± 0.076	0.046 ± 0.023
Diaptomus	15.2	52	7	1.2	12.7 ± 0.7	63 ± 3.3	34 ± 4	0.71 ± 0.13	0.022 ± 0.007
Holopedium	2.8	40	9	5.5	14.0 ± 2.1	145 ± 23	4 ± 1	0.88 ± 0.17	0.160 ± 0.020

* ♀♀ = adult females.

the different treatments (Table 1), we first examined the relationship between zooplankton species and biomass for our independent variables. The first step in this analysis was a test for constancy of slopes, which can be determined by examining the interaction term of a regression with zooplankton species treatment and zooplankton biomass as independent variables and the parameter values as dependent variables. In 8 of 10 cases we could assume that our slopes were not significantly different and proceeded with a full analysis of covariance (ANCOVA); that is, the probability value for our interaction term was not significant ($P > 0.05$). We then conducted full ANCOVAs with zooplankton treatment as an independent variable and zooplankton biomass as a concomitant variable. Individual zooplankton species treatments were declared significantly different from the control treatment based on the results of two-tailed Dunnett *t* tests. The ratio data (DIN/SRP, phaeophytin per chlorophyll *a*, relative primary production, bacteria biovolume per algal biovolume) were arcsine transformed while the remaining data (DIN, SRP, bacteria cell abundance, algal community structure and biovolume, total primary production, and ciliate and rotifer abundance) were $\log_{10}(X + 1)$ transformed. A multidimensional scaling procedure was carried out using SYSTAT version 4.0 (Wilkinson 1988) with transformed data (observation − parameter mean/parameter standard deviation), using the covariance option within the correlation module to generate similarity indices, and the multidimensional scaling module to generate a two-dimensional similarity plot. Multidimensional scaling is a clustering strategy using full dimensions, in this case two, whereas many other clustering strategies (e.g., dentograms) utilize more than one but less than two dimensions. The purpose of this procedure was to obtain an objective measure of similarity or dissimilarity between and within the treatments based on the results obtained for the measured parameters.

RESULTS

The four zooplankton treatments (*Diacyclops, Daphnia, Diaptomus, Holopedium*) began with individual abundances roughly equivalent to peak abundances previously noted for these species in Castle Lake (M. T. Brett, *personal observations*) (Table 1). Over 94% of the zooplankton biomass in each treatment consisted of the treatment species, with the remaining biomass made up almost exclusively of nauplii. During the experiment, biomass increased and fecundity decreased in each zooplankton species treatment. The increase in biomass in all treatments was due to the recruitment of juveniles, i.e., juveniles comprised 10–20% of treatment species biomass at the beginning of the experiment and generally >50% of treatment biomass at the end of the experiment.

The results of the ANCOVA analyses, with zooplankton species treatment as an independent variable and zooplankton biomass as a concomitant variable showed that the zooplankton species term was significant for every parameter presented in Table 2, while the zooplankton biomass term was significant in only one case (i.e., for the ratio of bacterial to algal biomass). In this case the variability explained by the biomass term was small, 12.2% of the sum of squares, compared to the variability explained by the zooplankton species term, 50.6% of the sum of squares. Thus, in general, our experimental results reflected the effect of zooplankton species treatments and not the disparities in zooplankton biomass between treatments.

While our ANCOVA analysis suggests zooplankton biomass was responsible for only a small portion of the treatment responses noted, relative to treatment zooplankter species, this does not mean that our results were unaffected by disparities in zooplankton biomass between treatments. For example, the *Diacyclops* and *Diaptomus* had final biomasses approximately one-third of those for the *Daphnia* and *Holopedium* treatments. Thus one would have logically expected greater treatment impacts in the *Diacyclops* and *Diaptomus* had they had the same biomass as the *Daphnia* and *Holopedium* treatments.

In order to mathematically compensate for disparities in zooplankton biomass between the different treatments we calculated zooplankton-induced deviation rates from the zooplankton-free control treatment. These treatment deviation rates were calculated for each zooplankton treatment and for all measured pa-

rameters according to the logistic growth equation, i.e., parameter : treatment deviation rate = [ln(treatment : replicate value) − ln(control mean)]/8. These values were then corrected for disparities in treatment biomass by multiplying the parameter : treatment deviation rate by the ratio of the zooplankton biomass in the *Daphnia* treatment and the zooplankton biomass in the *Diacyclops* and *Diaptomus* and *Holopedium* treatments. Treatment biomasses were normalized to the *Daphnia* values because *Daphnia* is the most commonly investigated freshwater zooplankter and because the *Daphnia* treatment achieved the highest biomass during this experiment. This data manipulation assumes that the relationship between the deviation rate and treatment zooplankton biomass is linear; this is probably true in most but not all cases (Carrick et al. 1991). In essence this approach is saying: if a hypothetical deviation rate is 0.30 and 0.10 in the *Daphnia* and *Diaptomus* treatments, respectively, and the *Daphnia* treatment had a 3 times greater biomass than did the *Diaptomus* treatment then the biomass corrected deviation rates would be 0.30 and 0.30 in the *Daphnia* and *Diaptomus* treatments, respectively. Instead of concluding that the responses to the two zooplankton species were different, correcting for biomass leads to the conclusion that the responses were similar. Since this data manipulation makes an assumption that may not be true (i.e., a linear relation between response and zooplankton biomass), we did not conduct a formal statistical analysis of these data.

The biomass-adjusted deviation rates (Table 3) suggest *Daphnia* had the greatest negative impact on total phytoplankton biovolume and enriched DIN (relative to SRP) the most of the zooplankton species tested. *Diaptomus* had the greatest positive impact on SRP concentrations, the ratio of phaeophytin to chlorophyll, and most strongly enriched SRP (relative to DIN) of the zooplankters tested. *Daphnia* and *Diaptomus* had similar strong positive impacts on DIN concentrations, relative primary production, and the ratio of bacteria to phytoplankton biovolume. *Diacyclops* very strongly depressed rotifer (almost exclusively *Polyarthra vulgaris*) and ciliate abundance, but had no notable effect on dissolved nutrients, the phytoplankton, or bacterioplankton relative to the control treatment. *Holopedium* generally had similar but weaker impacts, compared to *Daphnia* and *Diaptomus,* on all of the measured parameters (Table 3).

The treatment responses for the individual algal species were generally not as strong as the total phytoplankton biovolume response to the zooplankton treatments (Table 4). This is mainly because *Peridinium inconspicuum,* which strongly dominated total algal biomass, showed a strong response to grazing by *Diaptomus, Holopedium,* and *Daphnia,* while many of the rarer algal species only showed a strong response to grazing by *Daphnia.* Of the 10 algal species found in at least 80% of the samples, *P. inconspicuum, Arthrodesmus* sp., *Scenedesmus bijuga, Oocystis* sp., *Dictyosphaerium pulchellum, Rhodomonas minuta, Microcystis flos-aquae,* and small flagellates had reduced abundances in the *Daphnia* treatment. Of the common

TABLE 2. Results of an ANCOVA for the various parameters, with zooplankton species as a category variable and zooplankton biomass as a concomitant variable. The interaction probability value refers to the test for constancy of slopes.

Source of variation	ss	df	*F* ratio	*P*
DIN*				
Zooplankton species	0.625	4	8.79	0.0003
Zooplankton biomass	0.012	1	0.69	0.4177
Error	0.336	19	...	...
Interaction	...	...	...	0.9850
SRP†				
Zooplankton species	0.442	4	3.98	0.0165
Zooplankton biomass	0.007	1	0.25	0.6257
Error	0.528	19	...	...
Interaction	...	...	...	0.0390
DIN/SRP				
Zooplankton species	12.0	4	15.88	0.0001
Zooplankton biomass	0.11	1	0.56	0.4646
Error	3.59	19	...	...
Interaction	...	...	...	0.8540
Phytoplankton biomass				
Zooplankton species	0.416	4	8.48	0.0004
Zooplankton biomass	0.027	1	2.17	0.1572
Error	0.233	19	...	...
Interaction	...	...	...	0.0750
Phaeophytin/chlorophyll				
Zooplankton species	0.090	4	5.29	0.0050
Zooplankton biomass	0.004	1	0.85	0.3690
Error	0.081	19	...	...
Interaction	...	...	...	0.5770
^{14}C/phytoplankton				
Zooplankton species	0.00083	4	3.25	0.0340
Zooplankton biomass	0.00022	1	3.41	0.0810
Error	0.00122	19	...	...
Interaction	...	...	...	0.2040
Bacteria				
Zooplankton species	0.0228	4	4.26	0.0126
Zooplankton biomass	0.0005	1	0.36	0.5537
Error	0.0255	19	...	...
Interaction	...	...	...	0.3780
Bacteria/phytoplankton				
Zooplankton species	0.164	4	6.34	0.0020
Zooplankton biomass	0.038	1	6.30	0.0210
Error	0.123	19	...	...
Interaction	...	...	...	0.2320
Ciliates				
Zooplankton species	4.850	4	83.36	0.0001
Zooplankton biomass	0.037	1	2.54	0.1296
Error	0.247	17	...	...
Interaction	...	...	...	0.2060
Rotifers				
Zooplankton species	4.194	4	26.29	0.0001
Zooplankton biomass	0.139	1	3.49	0.0780
Error	0.718	17	...	...
Interaction	...	...	...	0.0220

* DIN = dissolved inorganic nitrogen.
† SRP = soluble reactive phosphorus.

TABLE 3. Zooplankton biomass adjusted treatment rates of deviation from controls. Values presented are mean ± 1 SD. Values for the removal treatment were not adjusted for zooplankton biomass.

Treatment	DIN*	SRP†	DIN/SRP	Algal biovol.	Phaeo./chl.
Removal	0.000 ± 0.062	0.000 ± 0.028	0.000 ± 0.062	0.000 ± 0.027	0.000 ± 0.017
Diacyclops	−0.017 ± 0.286	0.000 ± 0.028	−0.017 ± 0.286	0.030 ± 0.033	0.005 ± 0.065
Diaptomus	0.299 ± 0.098	0.115 ± 0.079	−0.428 ± 0.107	−0.109 ± 0.087	0.154 ± 0.079
Holopedium	0.086 ± 0.041	0.073 ± 0.049	−0.115 ± 0.055	−0.103 ± 0.037	0.048 ± 0.032
Daphnia	0.252 ± 0.054	0.057 ± 0.078	0.120 ± 0.037	−0.185 ± 0.078	0.045 ± 0.014

* DIN = dissolved inorganic nitrogen.
† SRP = soluble reactive phosphorus.

algae, *P. inconspicuum* and *Rhodomonas minuta* were most consistently reduced by zooplankton grazing. If these values were adjusted for disparities in zooplankton biomass between the different treatments, the expected impacts of the *Diacyclops, Diaptomus,* and *Holopedium* treatments would only be slightly greater.

A multidimensional scaling of the data presented in Figs. 1, 2, 3, and 4 shows that the zooplankton species treatments resulted in four distinguishable groupings (Fig. 5). One grouping each was noted for the control, *Diacyclops,* and *Daphnia* treatments and a fourth structure for the *Diaptomus* and *Holopedium* treatments combined. DIN, algal abundance, and the ratios of phaeophytin/chlorophyll *a,* ^{14}C uptake/algal carbon and bacterial biovolume/algal biovolume significantly loaded on Dimension 1, while bacteria biovolume, and ciliate and rotifer abundance significantly loaded on Dimension 2.

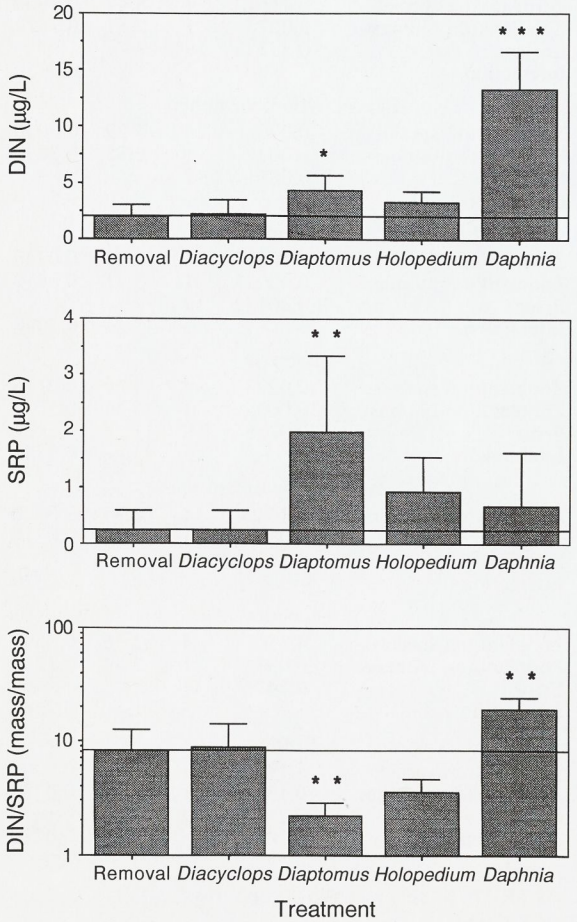

FIG. 1. The response of dissolved inorganic nitrogen (DIN), soluble reactive phosphorus (SRP), and the ratio of DIN/SRP to the zooplankton species treatments. The values presented are mean ± 1 SD, the Dunnett *t* test probabilities are $*P < 0.05$, $**P < 0.01$, and $***P < 0.001$.

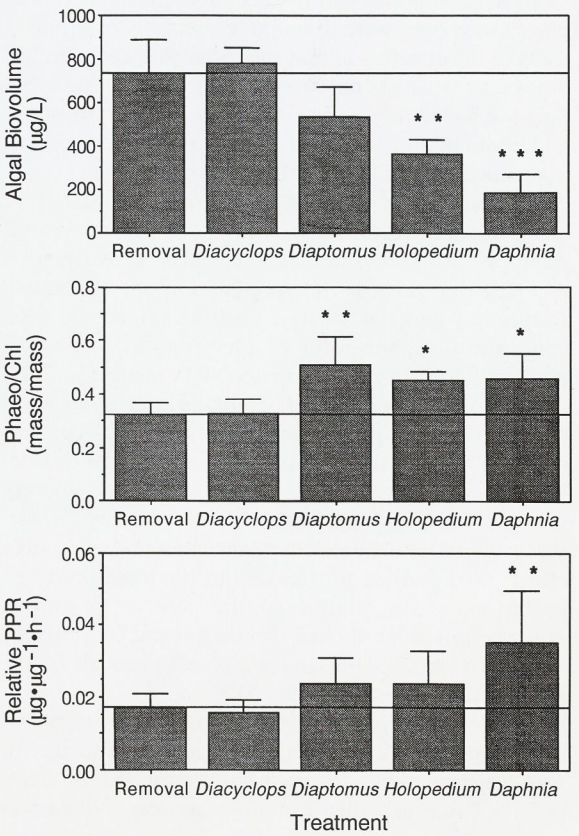

FIG. 2. The response of phytoplankton biovolume, the ratio of phaeophytin to chlorophyll *a,* and the ratio of CO_2 uptake to algal biomass to the zooplankton species treatments. Algal carbon content was assumed to be 16% of biovolume. See Fig. 1 for explanation of symbols. PPR = primary production.

TABLE 3. Continued.

Relative PPR	Bacteria	Bact./phyto.	Ciliates	Rotifers
0.000 ± 0.027	0.000 ± 0.023	0.000 ± 0.045	0.000 ± 0.021	0.000 ± 0.031
−0.033 ± 0.100	0.052 ± 0.055	0.022 ± 0.057	−1.180 ± 0.169	−1.140 ± 0.494
0.112 ± 0.096	0.054 ± 0.037	0.163 ± 0.099	−0.370 ± 0.137	−0.135 ± 0.223
0.046 ± 0.054	0.017 ± 0.015	0.121 ± 0.034	−0.126 ± 0.049	−0.087 ± 0.084
0.093 ± 0.070	−0.018 ± 0.008	0.167 ± 0.083	−0.240 ± 0.078	−0.048 ± 0.046

DISCUSSION

The zooplankters tested in this experiment can be divided into two broad ecological categories: (1) the carnivorous *Diacyclops* and (2) the omnivorous *Daphnia, Diaptomus,* and *Holopedium* (Figs. 1–4). The raptorial *Diacyclops* decimated the ciliate and rotifer microzooplankton, but had no notable effect on nutrient concentrations, bacterioplankton, phytoplankton, or primary production relative to zooplankton-free controls. The filter-feeding cladocerans *Daphnia* and *Holopedium* and the raptorial and filter-feeding calanoid copepod *Diaptomus* showed several effects typical of herbivores, such as increasing dissolved nutrient concentrations and decreasing algal biomass. However, these species also depressed microzooplankton abundance, particularly that of ciliates. None of the zooplankton treatments had an effect on bacterioplankton abundance. Multidimensional scaling, a fully two-dimensional clustering strategy, revealed four different planktonic ecosystem structures in response to our zooplankton species treatments. The removal, *Diacyclops,* and *Daphnia* treatments formed independent structures, while the *Diaptomus* and *Holopedium* treatments combined to form a fourth independent structure (Fig. 5). These results confirm that shifts in zooplankton community species composition should in and of themselves result in shifts in overall planktonic ecosystem structure.

In Castle Lake *Diacyclops* and *Holopedium* generally have their peak abundances in early summer, while the population peaks for *Daphnia* and *Diaptomus* can occur any time during the summer. Thus there could be regular shifts in the intensity of zooplankton–phytoplankton or zooplankton–microzooplankton interactions (e.g., due to *Diacyclops* and *Holopedium*) or erratic fluctuations in these interactions due to normal unpredictable population peaks for *Daphnia* and *Diaptomus.* Our results suggest the shift in crustacean zooplankton community structure, caused by our prior manipulation of the fish community, can be expected to have profound effects on the dissolved nutrient concentrations, phytoplankton, bacteria, and microzooplankton of Castle Lake. The increase in *Diacyclops* and decrease in *Daphnia* and *Diaptomus* abundance noted during the last several years should cause the crustacean zooplankton assemblage to change from primarily a grazer-dominated community to a community with much more carnivory. Consistent with these predictions, whole-lake monitoring (J. J. Elser, *personal observation*) has shown that water clarity (an inverse measure of algal biomass) decreased and total primary production increased at the same time that the zooplankton community structure shifted in Castle Lake.

Since our experiments were conducted during only one time period, one can question to what extent they are representative of the entire summer season. Research on the clear water phase (Lampert et al. 1986) has shown that the overall effect of zooplankton grazing on planktonic ecosystems is dependent on the composition of the algae, with strong zooplankton effects

TABLE 4. Algal species biovolume, μg/L, in each of the zooplankton species treatments, mean biovolume ± 1 SD is presented. Statistical differences were determined using two-tailed Dunnett *t* test results of logarithmically transformed data. Only data for those species observed in at least 80% of the samples are given.

	Removal	*Diacyclops*	*Diaptomus*	*Holopedium*	*Daphnia*
Peridinium inconspicuum	251 ± 37	278 ± 45	153 ± 19*	104 ± 33***	29.5 ± 23***
Arthrodesmus sp.	36.3 ± 8.9	37.2 ± 6.4	35.3 ± 8.7	28.0 ± 4.8	24.3 ± 11.3*
Scenedesmus bijuga	23.8 ± 14	25.6 ± 7.5	21.7 ± 15.9	9.2 ± 5.7	2.1 ± 3.0**
Oocystis sp.	9.2 ± 3.7	6.2 ± 5.5	6.6 ± 2.1	7.8 ± 2.6	4.7 ± 2.8*
Small flagellates	6.5 ± 2.9	5.7 ± 1.3	5.7 ± 1.5	5.5 ± 2.0	2.1 ± 1.1**
Dictyosphaerium pulchellum	4.1 ± 2.0	5.2 ± 5.1	5.7 ± 2.8	5.0 ± 2.6	1.2 ± 1.3*
Rhodomonas minuta	1.6 ± 0.9	2.0 ± 0.4	0.6 ± 0.1**	0.4 ± 0.2***	0.05 ± 0.03***
Synedra sp.	0.63 ± 0.12	1.34 ± 0.43**	1.00 ± 0.36	0.42 ± 0.13	0.51 ± 0.35
Microcystis flos-aquae	0.58 ± 0.37	0.38 ± 0.22	0.40 ± 0.22	0.41 ± 0.25	0.08 ± 0.10*
Dinobryon bavaricum	0.58 ± 0.39	0.33 ± 0.29	0.23 ± 0.30	0.47 ± 0.51	0.17 ± 0.14

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

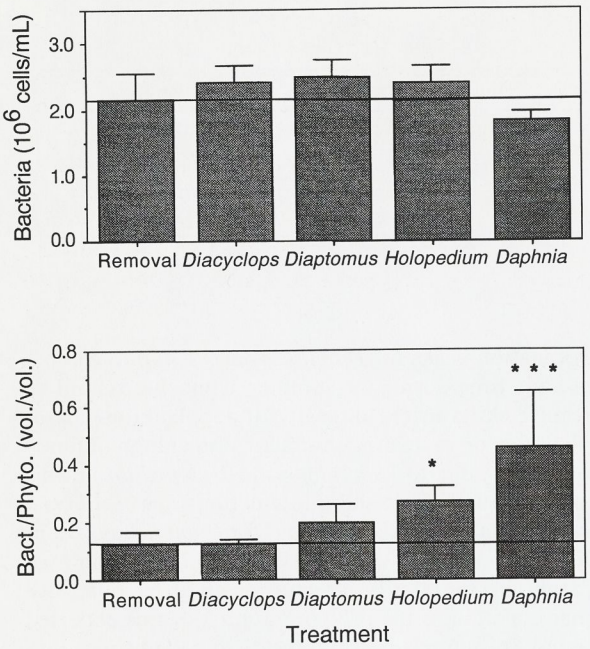

FIG. 3. The response of bacteria cell abundance and the ratio of bacterial biovolume to algal biovolume to the zooplankton species treatments. The volume of each bacteria cell was assumed to be 0.04 μm^3. See Fig. 1 for explanation of symbols.

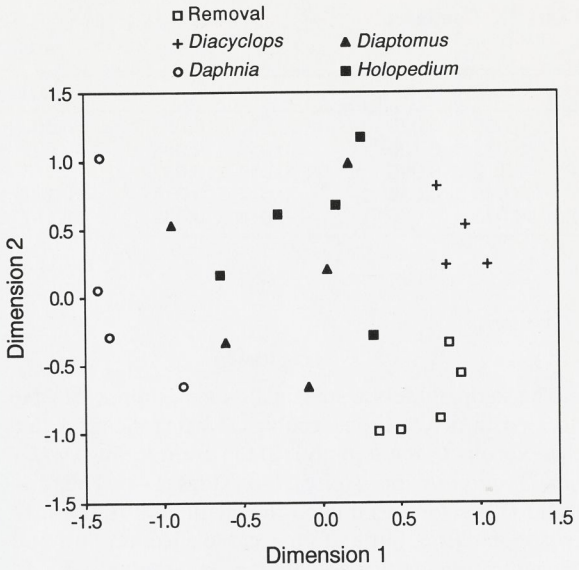

FIG. 5. Multidimensional scaling plot based on the planktonic community structure data presented in Fig. 1. The similarity matrix for this plot was generated using the covariance module of SYSTAT, using raw data transformed by subtracting the overall mean from the observation and dividing this product by the overall standard deviation. The purpose of this procedure was to obtain an objective measure of similarity or dissimilarity between and within the treatments based on the results obtained for the measured parameters.

expected when the phytoplankton is dominated by edible algae (e.g., diatoms and flagellates) and weak effects expected when the phytoplankton is dominated by grazing-resistant colonial forms or algae of poor nutritional quality (e.g., blue-greens) (Kerfoot et al. 1988). Generally speaking, the phytoplankton community of Castle Lake is rarely dominated by colonial forms, with the exception of a late-summer deep layer *Dinobyron* maximum, so zooplankton are likely to have a greater impact on the algae of this lake than in either ultraoligotrophic or hypereutrophic lakes (Elser and Goldman 1991).

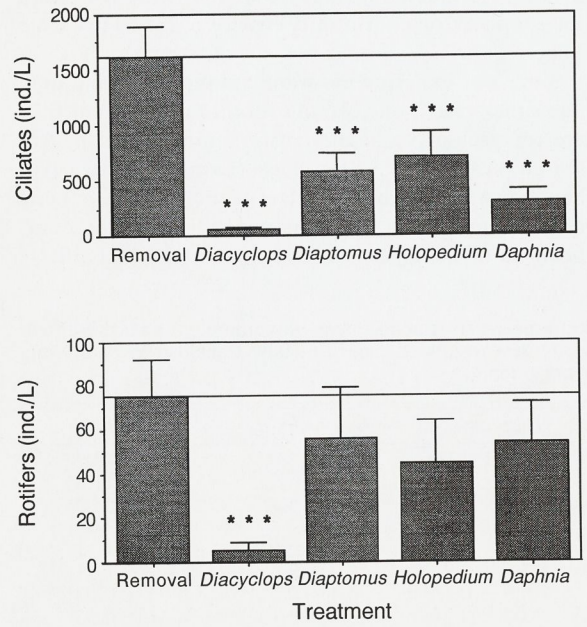

FIG. 4. The response of rotifer and ciliate abundance to the zooplankton species treatments. See Fig. 1 for explanation of symbols.

Classic characterizations such as carnivore and herbivore may not be completely appropriate for freshwater zooplankton, which are probably all omnivores to a greater or lesser extent. We know, for example, that *Diacyclops* severely depressed ciliate and rotifer microzooplankton abundance and had no notable effect on the algae, bacteria, or nutrient cycling, but we do not actually know whether *Diacyclops* only consumed microzooplankton. Regardless, the apparent effect of *Diacyclops* was exclusively that of a carnivore. This result was obtained despite the fact that much of the final zooplankton biomass in the *Diacyclops* treatment was composed of nauplii that are generally thought to be more herbivorous than cyclopoid copepodites and adults. Similarly, *Daphnia, Diaptomus,* and *Holopedium* may have reduced microzooplankton abundance through interference (direct physical interactions) or exploitative competition and not actually consumed them (Gilbert 1989), but their apparent roles were those of omnivores. Wickham and Gilbert (1993), however, suggest *Daphnia* suppression of microzoo-

plankton is due to interference and direct predation as opposed to exploitative competition. Certainly none of the zooplankters we examined could be classified as exclusively herbivorous based on our experimental results. Classic definitions are further complicated by the fact that a major component of planktonic ecosystems (i.e., the protozoa) are often mixotrophic, that is, they consume particles such as bacteria or small algae and can photosynthesize. Any animal that consumes a mixotroph should therefore be an omnivore. More than anything else, our results probably suggest that strict definitions such as carnivory and herbivory may not be completely relevant in planktonic ecosystems, where food particle selection by zooplankton is generally based on prey size, particle detection, taste, etc. (DeMott and Moxter 1991) and is probably only marginally constrained by whether the particle in question is auto- or heterotrophic.

The results of our ANCOVA analyses indicate that in each case there was a significant zooplankton species effect, while the zooplankton biomass term was only significant in one case, i.e., the ratio of phytoplankton to bacteria biomass. These results indicate that different zooplankters have varying effects on the parameters measured, but they say nothing about the relative importance of zooplankton species vs. zooplankton biomass in influencing planktonic ecosystem processes and structure. This is because there was little variation in zooplankton biomass within zooplankton species treatments, although there was variation between treatments. Namely, the *Daphnia* and *Holopedium* treatments had final biomasses ≈ 3 times larger than those for the *Diaptomus* and *Diacyclops* treatments. Had we used identical zooplankton biomasses for each treatment, we would have expected greater effects in the *Diaptomus* and *Diacyclops* treatments. Clearly, this experiment was not designed to assess the importance of zooplankton biomass for any of the zooplankton species tested. Elser and Goldman (1991) examined the relative importance of *Daphnia* and ambient zooplankton biomass on Castle Lake phytoplankton. They observed that experimental gradients of either ambient Castle Lake zooplankton or *Daphnia* caused reductions in algal biomass and increases in dissolved ammonia and relative primary production with increasing biomass.

When adjusted for dissimilarities in zooplankton biomass between zooplankton species treatments our data suggest *Daphnia* and *Diaptomus* had grazing impacts of similar magnitudes, while *Holopedium* had qualitatively similar but weaker grazing impacts. In general these species influenced planktonic ecosystem structure in a manner expected from trophic cascade theory (Carpenter et al. 1985), that is, these zooplankters increased free nutrient concentrations, depressed phytoplankton community biomass, increased relative primary production, and depressed microzooplankton abundance (Figs. 1–4). *Daphnia* also reduced the abundance of the algae *Peridinium inconspicuum, Arthrodesmus* sp., *Scenedesmus bijuga, Oocystis* sp., *Dictyosphaerium pulchellum, Rhodomonas minuta, Microcystis flos-aquae,* and small flagellates. In similarly designed studies, Pace and Funke (1991) found *Daphnia pulex* usually reduced ciliate abundance, occasionally reduced chlorophyll *a* concentrations and heterotrophic flagellate abundance, and had no effect on bacterial abundance and production. Wickham and Gilbert (1991) showed *Daphnia pulex* generally reduced rotifer and ciliate growth rates, while *Bosmina longirostris* and *Daphnia galeata mendotae* had little influence on microzooplankton. None of the zooplankton species examined in their experiments had a significant effect on phytoplankton or bacterial abundance.

Of all the treatments, *Diacyclops* had the greatest effect on the ciliate and rotifer microzooplankton (Fig. 4). This result should be qualified with a few caveats. Namely, since we removed many other zooplankters such as nauplii, *Bosmina,* and juvenile *Daphnia,* which could have conceivably been the preferred prey for *Diacyclops,* from the lake water before starting the experiment, our results may not actually reflect the true effect of *Diacyclops* predation on typical zooplankton communities. Further, many prey species avoid predation by decreasing spatial overlap with their main predators (Williamson and Stoeckel 1990). However, since we enclosed both the microzooplankters and *Diacyclops* we prevented this possible prey escape mechanism. Our results probably exaggerated the typical effect of *Diacyclops* predation on microzooplankton communities.

While our experiment was not designed to explicitly test whether large body sized zooplankters have greater grazing impacts, as is commonly thought, a few observations are obvious. For example, *Diacyclops,* which was the smallest sized zooplankter examined (and which also had the smallest biomass), had the greatest impact on the microzooplankton, while *Daphnia* and *Diaptomus* generally had greater impacts on the measured parameters than the larger sized *Holopedium.* In contrast, Pace (1984) found that zooplankton biomass explained little residual variability for total phosphorus to chlorophyll relationships, while mean zooplankton biomass explained a significant amount of residual variability. Similarly, Vanni (1987) found an increase in mean zooplankton size and total community biomass, due to reduced fish predation, resulted in a decrease in total algal biomass, reductions in the abundance of edible algae, and a shift towards grazing-resistant algae. However, a more comprehensive investigation (90 zooplankton communities from 28 lakes) of the importance of zooplankton size (Cyr and Pace 1993) found only a weak relationship ($r^2 = 0.15$) between mean zooplankter body mass and zooplankton community grazing rate. These authors suggested grazing differences among zooplankton taxa may be a

potentially important source of variability in this relationship. This is supported by observations of particle selection, which show far greater differences between zooplankton taxa than simple body size relations would suggest (Hessen 1985, DeMott 1986, DeMott and Moxter 1991).

To examine nutrient cycling and experimentally test the predictions of stoichiometric theory (Sterner et al. 1992), we measured the effects of the different zooplankton species on the DIN/SRP ratio (Fig. 1). *Diaptomus* disproportionately increased SRP relative to DIN, resulting in a low DIN/SRP ratio in this treatment. In contrast, *Daphnia* increased DIN relative to SRP, resulting in a high DIN/SRP ratio. These observations are consistent with recent work on the stoichiometry of N and P recycling by crustacean zooplankton (Sterner et al. 1992). According to stoichiometric theory, animals with low body N:P ratios should recycle nutrients at high N:P ratios relative to their food, while high N:P animals should regenerate at low ratios. Andersen and Hessen (1991) reported that *Daphnia* had a characteristically low N:P ratio and *Diaptomus* had a high N:P ratio. Our results for *Diacyclops* (no difference from the control treatment) are also consistent with stoichiometric theory since it is predicted that carnivores will consume food with elemental ratios similar to their own. This means carnivores will excrete few nutrients and these nutrients will be excreted at the ratio at which they were consumed (Brett 1993). Since *Holopedium* has a low body N:P ratio (Andersen and Hessen 1991), stoichiometric theory predicts this species will regenerate nutrients at a high N:P ratio, however, in contrast to theory, our data suggested that *Holopedium* regenerated relatively more SRP than DIN. Thus our results support stoichiometric predictions for three of the four zooplankters examined.

In contrast to many terrestrial investigations, our study did not show stimulation of total primary production in any of the zooplankton species treatments (in fact it was depressed in the *Daphnia* and *Holopedium* treatments), however relative primary production was stimulated in the *Daphnia* treatment (Fig. 2). Total primary production is algal production per volume lake water while relative primary production is algal production per unit algal biomass. Since zooplankton grazing should release nutrients, grazing could in theory stimulate the growth of those algal cells not grazed provided the algal community is nutrient limited. Thus grazing may depress total community production but stimulate the relative production of the surviving plants. The results of the present experiment showing depressions of total primary production and stimulation of relative primary production in some treatments are in contrast to those of Bergquist and Carpenter (1986), who found that total primary production was positively correlated with zooplankton biomass in grazing experiments. However, our findings are essentially the same as those of Svensson and Stenson (1991), who found reductions in total primary production and increases in relative primary production, and Uehlinger and Bloesch (1987), who found reductions in total primary production in response to zooplankton grazing. The present study is also consistent with two previous experiments from Castle Lake (Elser and Goldman 1991, Elser 1992), which found that ambient concentrations of zooplankton decreased total primary production and increased relative primary production. Thus zooplankton grazing does not usually stimulate total phytoplankton primary production, but it may often increase relative primary production.

Similar to phytoplankton, planktonic bacteria are limited by nutrients (particularly phosphorus) and are grazed by heterotrophic flagellates, ciliate and rotifer microzooplankton, and crustacean zooplankton. Since bacteria are generally smaller than algae they are thought to be grazed more by heterotrophic flagellates and microzooplankton, while algae are usually assumed to be grazed mostly by the larger crustacean zooplankton. Unlike most algae, bacteria derive their energy from the breakdown of organic compounds. Crustacean zooplankton may depress bacteria abundance by directly consuming them. In contrast, crustacean zooplankton may also stimulate bacterial standing stocks by depressing phytoplankton biomass thereby reducing nutrient competition between bacteria and algae, by depressing microzooplankton bacteria grazers, and by releasing organic compounds while feeding. The measured bacterial abundances for the four zooplankton treatments were never significantly different from the zooplankton removal treatment (Fig. 3). However, the *Diacyclops, Diaptomus,* and *Holopedium* treatments stimulated bacterial standing stock sufficiently and the *Daphnia* treatment depressed algal standing stock enough to result in the *Daphnia* treatment having significantly lower bacterial cell abundance than observed in the *Diacyclops, Diaptomus* and *Holopedium* treatments ($P < 0.01$). These data could be used to argue against a direct coupling between crustacean zooplankton grazing and bacterial abundance, in agreement with Pace and Funke (1991) and Wickham and Gilbert (1991) and in contrast to Riemann and Søndergaard (1986), if we use the control treatment as a frame of reference. However, if we base our conclusions on differences between the zooplankton treatments, there is evidence that *Daphnia* grazing may have reduced bacterial standing stocks, while *Diacyclops, Diaptomus,* and *Holopedium* stimulated the bacterioplankton. The latter conclusions are at least consistent with the feeding morphologies of these zooplankters (Hessen 1985), i.e., *Daphnia* are able to filter the smallest particles. Since *Daphnia* depressed phytoplankton biomass much more than they depressed bacteria abundance, *Daphnia* actually shifted the ratio between bacterial and algal biomass in the direction of the bacteria to a far greater extent than did the other zooplankton treatments. This

result may reflect food preferences and feeding morphologies or it may simply be due to the fact that *Daphnia* also depressed micozooplankton, and possibly other heterotrophs, which are important consumers of bacteria.

The present investigation indicates the raptorial cyclopoid copepod *Diacyclops* was mainly carnivorous and decimated the microzooplankton. The filter-feeding cladocerans *Daphnia* and *Holopedium* and the raptorial and filter-feeding calanoid copepod *Diaptomus* were apparently omnivorous. These species regenerated nutrients, and depressed phytoplankton food and microzooplankton competitors. Coupled with our field observations indicating *Diacyclops* has greatly increased its abundance and *Daphnia* and *Diaptomus* have decreased their abundances during time preceding these experiments, our experimental results suggest Castle Lake should have entered a period in which grazing on the microzooplankton increased markedly, and phytoplankton biomass and total primary production increased. Consistent with these predictions, whole-lake monitoring (J. J. Elser, *personal observation*) has shown that water clarity (a measure of algal biomass) decreased and total primary production increased at the same time that the zooplankton community structure shifted in Castle Lake. These observations suggest seasonal and interannual changes in crustacean zooplankton community structure, brought about by interactions with planktivore communities or due to normal seasonal succession, should in turn have profound influences on the structure of the planktonic ecosystems.

Acknowledgments

This study was funded by National Science Foundation grants BSR-9006623 and BSR-8918448 to C. R. Goldman, and BSR-9017579 to J. J. Elser. We thank W. R. DeMott, G. Malyj, P. King, and C. Luecke for their comments on this manuscript.

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State of California

Memorandum

To : Chuck Cesena, Cal Trans Date : Sep 6, 1994

From : **Department of Fish and Game**

Subject: Rincon Creek Surveys

This is in response to your request for information regarding steelhead/rainbow trout in Rincon Creek. The result of two surveys this year indicate that rainbow trout/steelhead have been extirpated from Rincon Creek. Surveys done on adjacent streams have provided different results: a stream survey done on Carpinteria Creek last month by the Department of Fish and Game's (DFG) wild trout stream survey crew found a relatively abundant population of rainbow trout, despite the fact that fish habitat quality in Carpinteria Creek appeared to be less (lower flows and less canopy) than that of Rincon Creek. We have also surveyed Steer Creek, a tributary to Carpinteria Creek, and found that it sustains a relatively large population of rainbow trout. Similar to Rincon Creek, the surveys in the Carpinteria Creek drainage failed to find other fish species that are native to streams in this area.

The absence of rainbow trout/steelhead in Rincon Creek and the absence of other native fish species in both Rincon and Carpinteria systems suggest that a catastrophic event eliminated fish populations from these systems within recent history. In 1985, the Wheeler Gorge Fire extended into the western portion of the Santa Ynez Mountain Range. The fire destroyed both upland and riparian vegetation in the Rincon and Carpinteria creek watersheds, burning 40% and 30% of the watersheds, respectively. Subsequent storms transported and deposited tons of sediment into the stream channels. The Romero fire in 1971 was even more catastrophic: it burned approximately 90% of the Carpinteria Creek watershed.

The Wheeler Fire could have been the event that eradicated rainbow trout from Rincon Creek, although there is anecdotal information from a landowner along Rincon Creek that suggests that the population was extirpated as early as the 1960's. There is documentation of rainbow trout/steelhead in this system in the 1950's and earlier.

In southern California, the alteration of habitat and localized extinctions resulting from fires and other natural disasters should be viewed as natural and recurring events. The key to persistence of southern California steelhead populations is the ability to recolonize affected habitat, when suitable conditions are reestablished. Adult steelhead from unaffected populations in nearby stream systems serve as donor populations. Adult steelhead are known to stray from their natal streams to spawn in nearby streams and it is believed that in hydrologically variable streams of southern California, straying is more prevalent than in less variable streams in more northern latitudes. This is one mechanism that has allowed steelhead to persist in the variable environment of southern California, provided that unimpeded access to headwaters is maintained. The presence of rainbow trout in the Carpinteria Creek system, which does not have significant barriers to steelhead migration, indicates that the streams in this area can support rainbow trout/steelhead populations if migration corridors are not blocked and recolonization is allowed to occur.

It appears that the Highway 101 culvert has prevented the recolonization of rainbow trout/steelhead in Rincon Creek. The upper reach of Rincon Creek appears to have adequate habitat to support rainbow trout/steelhead populations: there is adequate summer flow, it is well-shaded with an intact riparian zone, and it does not have the sedimentation problem that exists in the lower reach below the confluence with Casitas Creek. Abundance of aquatic invertebrates and amphibians in the upper reach indicates that the stream is highly productive and has good habitat quality.

The results of these surveys underscore the need to remove or modify the barrier to steelhead migration at the Highway 101 culvert on Rincon Creek. Habitat quality, persistence of flows in the upper reaches during the summer, and existence of rainbow trout in nearby stream systems indicate that rainbow trout/steelhead populations can be maintained in this system if recolonization is allowed to occur.

There are other, less significant migration impediments on this system, most notably several low-flow road crossings above the confluence with Casitas Creek. Also, U.S. Forest Service personnel have identified the reach just below the confluence with Casitas Creek as a potential barrier due to sediment input from Casitas Creek. I do not believe that these are as significant or absolute as the barrier at the Highway 101 culvert, however. It is likely that these areas are passable during periods of high flow, which is the preferential period for adult steelhead migration. Nevertheless, the delay or hinderance of adult steelhead caused by these impediments can reduce spawning success, therefore these problems will need to be addressed. I believe, however, that modification of the Highway 101 culvert is absolutely essential if restoration of the steelhead population in Rincon Creek is to be achieved.

Attached is the stream survey report for Carpinteria Creek. Maurice Cardenas will send the Rincon Creek and Steer Creek stream survey reports when they become available. If you have any questions, you can contact me at (916) 653-9442.

Dennis McEwan
Associate Fishery Biologist
California Department of Fish and Game

attachment

cc: Maurice Cardenas, DFG Santa Barbara
Steve Parmenter, DFG Bishop
Natasha Lohmus, DFG Long Beach
Dwayne Maxwell, DFG Long Beach
Tim Curtis, DFG Sacramento
George Heise, DFG Sacramento

Sara Chubb, Las Padres National Forest
6144 Calle Real
Goleta, CA. 93177

Mark Capelli, California Coastal Commission
89 S. California St.
Ste. 200
Ventura, CA. 93001

File #: Rincon Creek stream file (Santa Barbara County)

State of California

Memorandum

To : Ms. Nancy Vierra
Budget Branch

Date : July 1, 1996

From : Department of Fish and Game

Subject : Rincon Creek Culvert Modification Capital Outlay Budget Change Proposal for FY 1997-98

Attached is subject Capital Outlay Budget Change Proposal (COBCP) to partially fund construction work to modify the Rincon Creek - Highway 101 culvert, to restore steelhead access to upstream spawning and rearing habitat. We believe that implementation of a fish passage facility at this barrier will further the Department's goals for restoration of steelhead populations of southern California. Modification of the existing culvert is the most economically and biologically feasible alternative for restoring steelhead access to their historical spawning and rearing habitat.

Due to the Proposition 70 spending limitations, we believe that it is necessary to include this in the FY 1997/98 budget if the project is to be funded from the Wild Trout/Native Steelhead Account. There is widespread support for this project among Federal, State, and local agencies, and constituent organizations.

If you have any questions or concerns, please contact me at 653-6194, or Mr. Dennis McEwan, Associate Fishery Biologist, at 653-9442.

Eugene Flemenz

for Timothy C. Farley, Chief
Inland Fisheries Division

Attachment

cc: Ms. Antoinette Lobo
Department of Fish and Game
Sacramento, California

Mr. Chuck Cesena
Department of Transportation
San Luis Obispo, California

cc: Mr. Mark Capelli
California Coastal Commission
Ventura, California

Department of Fish and Game
Sacramento, California.

Mr. Alan Baracco - w/o attachment
Mr. Dennis McEwan - w/o attachment
Mr. Chuck Knutson - w/o attachment
Mr. George Heise - w/o attachment

Dr. Dwayne Maxwell - w/o attachment
Department of Fish and Game
Long Beach, California

Mr. Maurice Cardenas - w/o attachment
Department of Fish and Game
Santa Barbara, California

Mr. Steve Parmenter - w/o attachment
Department of Fish and Game
Bishop, California

Mr. Brian Trautwein - w/o attachment
Santa Barbara Urban Creeks Council
Goleta, California

Ms. Sara L. Chubb - w/o attachment
U S D A Forest Service
Goleta, California

Issue #_____

CAPITAL OUTLAY
BUDGET CHANGE PROPOSAL (COBCP)
FOR
FISCAL YEAR 1997-98

Organization Code: 3600	Department: FISH AND GAME
Project Title: Rincon Creek Culvert Modification	
Statewide Project Code:	Project Type:
This Proposal: $350,000 Phase: Construction	Fund Source(s): Proposition 70
Location: Rincon Creek at Highway 101 Overcrossing at the Ventura-Santa Barbara county line	Legislative Districts: Senate# 18 Assembly # 35 Congress: #22

Problem Statement: The Highway 101 culvert near the mouth of Rincon Creek is a complete block to migrating adult steelhead. Nearly 100% of the historical steelhead spawning and rearing habitat, much of which is still intact and capable of supporting a steelhead population, is located above this structure. As a consequence of this structure, steelhead/rainbow trout no longer exist in Rincon Creek. Reestablishment of steelhead in southern California streams is a high priority of the Department, as stated in the recently adopted *Steelhead Restoration and Management Plan for California*.

Proposal: To modify the existing culvert and install a second culvert to allow adult steelhead to access their historical spawning and rearing habitat.

Funding:

Fiscal Data (in thousands)

Phase	Prior Yr Funded	This Request	Future Years	Scheduled Completion Month/Year
Study				
Acq.				
P/P				
W/D				
Const		350		06/98
Equip				
Other(Specify)				
Total Cost				

Revision: (Yes/No)	Date Revised:	OPDM Estimate #:
Prepared by: Dennis McEwan Date: 7/1/98	Reviewed by: Date:	
Department Director: Date:	Agency Secretary: Date:	

Form DF-14E (Rev. 2/96)

PROGRAM NEED/PHYSICAL DEFICIENCY:

Southern steelhead (those occurring south of San Francisco Bay) were formerly found in coastal drainages as far south as northern Baja California. At present, Malibu Creek in Los Angeles County is the southern-most stream containing a known spawning population. Southern steelhead stocks are the most jeopardized of all of California's steelhead populations: numbers have declined drastically in nearly all southern streams. In the early 1960s, the Department estimated an annual spawning escapement to be about 60,000 adults for coastal areas south of San Francisco Bay. Currently, total number of adults for this area is unknown, but is probably on the order of 1,000 fish.

Major impacts to southern steelhead populations are from urbanization and other watershed disturbances, blocked access to headwater spawning and rearing areas, and partial and total dewatering of streams by water diversions and groundwater pumping. Water development, including dam construction, appears to be the primary cause of localized extinctions and decline in numbers within southern steelhead populations. A review of Department and other agency files indicates, that of 165 southern steelhead populations for which there is known historical information, 21% were impacted by barriers that blocked access to spawning and rearing habitat. Most of the remaining southern steelhead stocks are on the verge of extinction.

Rincon Creek historically supported a steelhead population. Although small, Rincon Creek is one of many streams along the Santa Barbara County coast that supported small, but viable, populations of steelhead. Most of these streams no longer support steelhead populations due to habitat alteration or inaccessibility. The construction of highway structures in the lower reaches of Rincon Creek has resulted in migration barriers which have blocked access to historical spawning and rearing areas.

The principal barrier is a large, impassable culvert through which Rincon Creek passes underneath the Highway 101 freeway immediately upstream of the stream's confluence with the ocean. This culvert completely blocks migrating adult steelhead from 100% of the historical spawning and rearing areas of Rincon Creek. Separate surveys by the Department and the Los Padres National Forest have shown that several miles of high-quality habitat still exists, much of which is well-protected within the Los Padres National Forest. Providing passage at the Highway 101 culvert could allow adult steelhead to again utilize this habitat.

Providing fish passage at the Highway 101 culvert is specifically recommended in the Department's *Steelhead Restoration and Management Plan for California* (Steelhead Plan). The Steelhead Plan identifies restoration of southern steelhead populations as the highest priority for steelhead management. Southern steelhead are a Department of Fish and Game Species of Special Concern. In addition, they are a candidate species for listing under the Federal Endangered Species Act. Providing passage at this structure would allow steelhead to recolonize historical habitat through natural straying of adults or through reintroduction by the Department.

Providing passage at the Highway 101 culvert is part of an effort to facilitate the reestablishment of a steelhead population in Rincon Creek. As mitigation for replacement of two highway bridges on Rincon Creek upstream from the Highway 101 culvert, the California Department of Transportation (Caltrans) is planning to correct the fish passage problems caused by the existing bridges. Because the barrier at the Highway 101 culvert is located downstream of these structures, the ultimate success of this mitigation project is contingent upon the restoration of access at the Highway 101 culvert, therefore, these two projects are indirectly related.

Restoration of the Rincon Creek steelhead population would be consistent with efforts and objectives of the Department, U.S. Fish and Wildlife Service, Los Padres National Forest, the National Marine Fisheries Service, and constituent organizations such as California Trout and the Santa Barbara Urban Creeks Council.

ALTERNATIVES:

1. Modify the existing culvert to provide passage for adult steelhead. The modifications would be made to the inlet and floor of the existing 18 feet wide by 21 feet high by 850 feet long concrete culvert. Once the culvert is able to pass fish, the preferred scenario would be to allow steelhead from nearby populations to recolonize the 'new' habitat naturally. If this does not take place in a reasonable amount of time, then artificial means, such as artificial spawning and rearing or hatch boxes, will be used to reintroduce steelhead into Rincon Creek.

2. Implement Trap-and-Truck Operation. This alternative would require that adult steelhead be trapped at the mouth of Rincon Creek and trucked around the culvert to a suitable location upstream.

3. Remove Culvert. This would entail removing the culvert and constructing another structure, such as a bridge, over which the Highway 101 roadway could pass.

SCOPE DESCRIPTION:

The configuration and slope of the existing Highway 101 culvert, particularly the inlet structure, prevents fish passage. Department engineer George Heise has developed a preliminary design to ameliorate the blockage, which consists of a series of baffles to lessen the effect of the steep inlet and to provide resting areas in the length of the culvert so that fish can pass through areas of high water velocity.

Caltrans originally agreed to modify the existing culvert in accordance with the preliminary plans supplied by the Department. These modifications were expected to cost approximately $200,000. Subsequent studies indicated that the proposed modifications would reduce the Highway 101 culvert's capacity by about 10%. Because the culvert already lacks the capacity to convey floodwater from a 100-year storm, Caltrans is unwilling to modify the existing culvert without implementing a means to offset this 10% loss of hydraulic capacity. They have proposed that a second 850 foot long culvert be installed to compensate for the loss of capacity due to the installation of baffles in the existing culvert.

The Department will enter into a contract with Caltrans to provide them with funds to modify the culvert to the Department's specifications. Before funds are distributed, we will obtain a written agreement with Caltrans that they will maintain and repair the culvert modifications as necessary. The Santa Barbara Urban Creeks Council, a non-profit volunteer-based organization, has agreed to provide labor for periodic debris removal efforts once the modifications are made.

DEPARTMENT EVALUATION/COST ESTIMATE:

Alternative 1 (culvert modification) is the best solution to providing fish access to their historical spawning and rearing areas. Caltrans estimates that the total cost of the project, including culvert modifications and installation of a second culvert, will cost $550,000. Caltrans is still committed to providing $200,000 for the project from District Highway funds and is seeking an additional $350,000. Because the culvert is a Caltrans facility, there will be no future fiscal impact to the Department for operation and maintenance.

Alternative 2 (Trap-and-Truck) is the least favorable alternative. This alternative would require that steelhead be trapped at the mouth of Rincon Creek (downstream of the culvert) and trucked to a suitable location upstream. Facilities and provisions that would be necessary if this alternative is to be considered are:

- Construction of a trapping facility downstream of the culvert. This would probably entail the construction of a temporary weir with permanent footings and foundations, a short fish ladder, and a permanent holding facility.
- Identification and access to a location and possible construction of a facility to release the steelhead at a safe distance upstream of the dam.
- Funding for operations and maintenance and probably two staff positions to operate and maintain the trapping facility and to transport fish to the release site. These personnel could be headquartered at Fillmore Hatchery.
- Purchase of a fish transport truck.

From a biological perspective, intensive handling and intervention in the life cycle of the fish makes this an undesirable alternative. In addition, trap-and-truck operations have failed to maintain anadromous fish stocks where they have been implemented in California (Nicasio Creek, Matilija Creek, and the Carmel River are a few notable examples) and we know of no examples where this type of passage facility has proven to be a success. For this reason, the Department's *Steelhead*

Rainbow Trout Management Policy (as stated in the Steelhead Plan) states that "...trap-and-truck operations will only be considered if there are no other feasible alternatives."

Alternative 3 (culvert removal) is probably the best solution from a fish passage perspective, but is the most infeasible of the three alternatives. This alternative would entail that some other structure be built, most likely a bridge, over which the roadway would pass. Because Highway 101 where it passes over Rincon Creek is a multi-lane freeway, the structure would need to be large enough to accommodate this, and would undoubtedly have a multi-million dollar cost.

IMPACT ON SUPPORT BUDGET:

Alternative 1 would have the least impact on the Department's budget. The funds will be passed through the Department to Caltrans to fund the project. Because Caltrans will maintain the culvert, there will be no future fiscal impact to the Department's support budget for this purpose. There may be a small impact if reintroduction of steelhead by artificial means becomes necessary.

COST/BENEFIT SOLUTION:

Alternative 1 is the best solution to the problem of blocked access for steelhead at the Highway 101 culvert. This alternative is the least intrusive and disruptive to the fish's life cycle, has the greatest chance of success, and is the most cost effective. $350,000 will be provided to Caltrans by the Department to construct, to the Department's specifications, culvert modifications to allow fish passage. This will allow steelhead to access their historical spawning and rearing habitat in the Rincon Creek system, thereby recovering the Rincon Creek population.

Environmental Compliance Information
Minor Capital Outlay Projects FY 1996-97

Please complete the following information:

Date 7/1/96

Project Name RINCON CREEK CULVERT MODIFICATION Region _____

Division IFD

Contact Person DENNIS MCEWAN Phone # 916.653.9442
(responsible for securing environmental compliance for the above project)

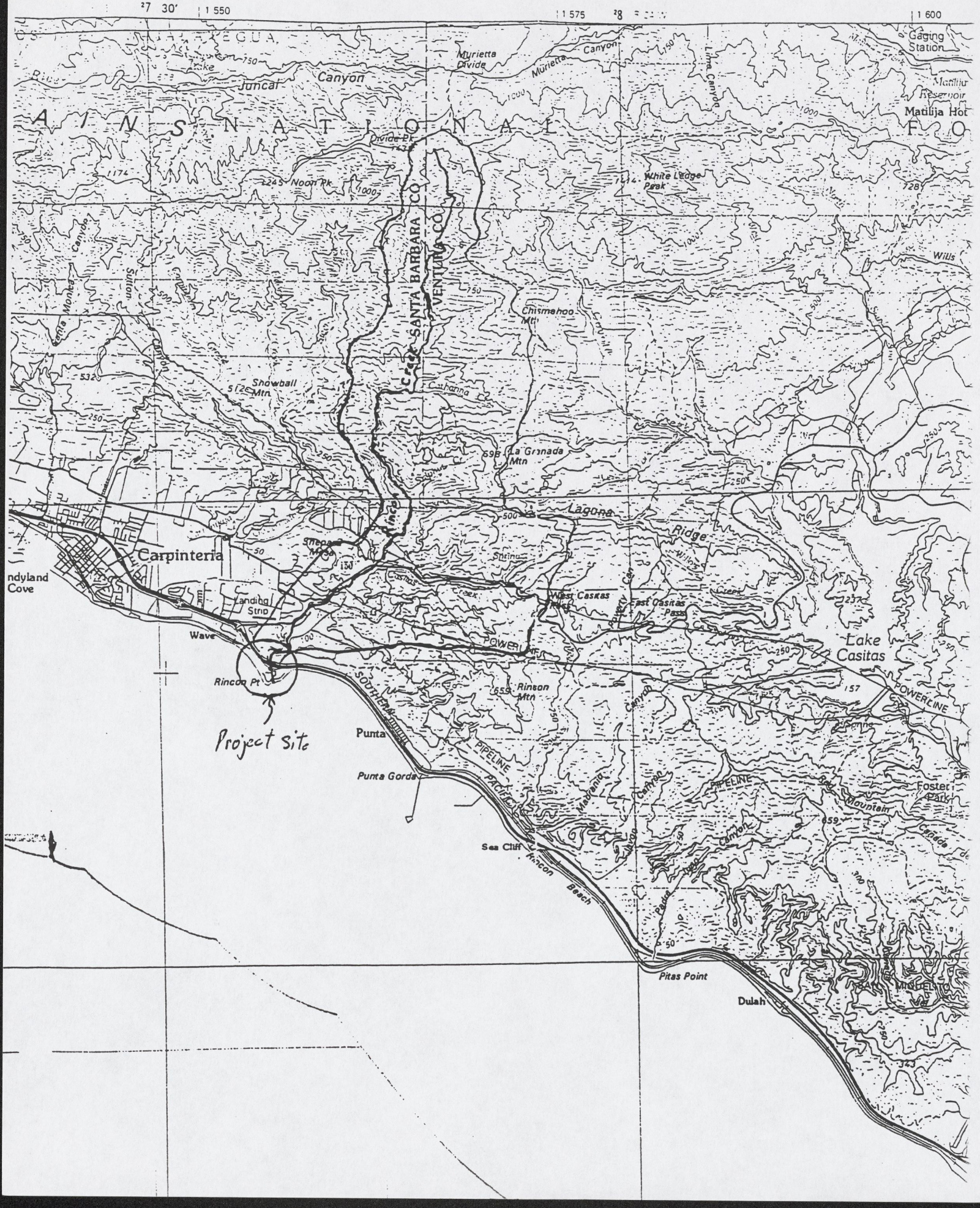
Project is (check one):

__XX__ Categorically exempt. Has process to obtain been started? Yes__ No__X__

_____ Other, state type of compliance to be obtained _____

Has process to obtain been started? Yes____ No____

_____ Environmental Compliance completed. Attach to COBCP.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Gaging Station
Matilija Reservoir
Matilija Hot
Juncal
Canyon
Murietta Divide
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Lime Canyon
Divide Pk
Noon Pk
White Ledge Peak
Wills
Chismahoo Mt
Santa Monica
Snowball Mtn
Cathanna
La Granada Mtn
Lagona Ridge
Carpinteria
Landing Strip
Wave
Rincon Pt
Project site
West Casitas Pass
East Casitas Pass
Lake Casitas
POWERLINE
Rincon Mtn
SOUTHERN PACIFIC PIPELINE
Punta
Punta Gorda
Sea Cliff
Rincon Beach
Pitas Point
Dulah
Foster Park
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Canada
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EFFECTS OF FOOD WEB COMPENSATION AFTER MANIPULATION OF RAINBOW TROUT IN AN OLIGOTROPHIC LAKE[1]

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Abstract. Stocking of the dominant planktivore of Castle Lake (rainbow trout) was discontinued to examine the impact of food web interactions on zooplankton communities and inter- and intra-annual dynamics of ecosystem properties (light penetration, primary productivity). Dynamics of zooplankton and ecosystem processes were examined for 3 yr following the manipulation and compared to 2–3 yr of premanipulation data. Sampling of vertebrate and invertebrate planktivores documented shifts in other members of the zooplanktivore guild as rainbow trout declined. Reduction of rainbow trout densities led to compensatory responses in other components of the Castle Lake fish assemblage as brook trout and golden shiners increased in abundance. This compensation resulted in increased rates of vertebrate planktivory on daphnids within 2 yr after trout stocking was discontinued. Zooplankton shifts in response to discontinuance of trout stocking were more rapid, particularly an immediate increase in a previously rare invertebrate predator (*Diacyclops thomasi*). Other limnological parameters also responded rapidly following the manipulation: water transparency declined and primary productivity (PPr) increased. In addition, intra-annual patterns (i.e., seasonal development) and the vertical distribution (shallow vs. deep) of PPr appeared to be affected by the food web manipulation. Our results indicate that complexities of real food webs complicate the prediction of the outcome of food web perturbations. Reduction of the previously dominant planktivore (rainbow trout) led to increases in other zooplanktivores (*Diacyclops,* golden shiners, brook trout) that resulted in enhanced predation pressure on zooplankton herbivores. Our results also indicate that alterations in water quality parameters (transparency, PPr) in response to food web alterations need not necessarily be mediated through changes in the abundance of *Daphnia,* as strong limnological responses preceded reductions in *Daphnia* by a year. We hypothesize an alternative mechanism for food-web-induced changes in lake ecosystem dynamics: changes in water clarity and productivity can result when cyclopoid predation strongly affects micrograzers.

Key words: cascading trophic interactions; ecosystem variability; food web compensation; lake food webs; primary productivity.

INTRODUCTION

The idea of "Cascading Trophic Interactions" (or CTI; Carpenter et al. 1985) has provided a conceptual framework for understanding the impact of higher trophic levels on ecosystem dynamics. Since the publication of that paper, a rapidly expanding number of studies has demonstrated that fish, through their effect on zooplankton, affect various aspects of ecosystem function (Leibold 1989, Carpenter and Kitchell 1993, Hairston and Hairston 1993). Tests of these ideas have also been extended to terrestrial ecosystems (Spiller and Schoener 1990, 1994). The CTI hypothesis, as originally formulated, placed the many components of complex pelagic food webs into dominant trophic levels consisting of piscivores, zooplanktivores, large and small zooplankton, and phytoplankton. While the compression of pelagic food webs into distinct trophic levels has considerable heuristic value, ecologists recognize that the components of real food webs are not readily categorized into distinct trophic levels (Cousins 1987). It remains an open question whether natural food webs function as predicted by CTI, especially when food webs are altered (Kerfoot and DeAngelis 1989).

One critical issue regarding whether changes in top predators propagate to cause substantial changes at the primary producer level involves the extent to which predators at the top of the food web segregate functionally into strong trophic interactors (sensu Paine

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1980) or whether compensatory shifts among multiple predator–prey species attenuate changes in predator abundance (Power 1992, Strong 1992, Hairston and Hairston 1993). Several conceptual approaches have been developed to analyze this type of trophic complexity. Kerfoot and DeMott (1984) refer to "dependent chains" and "vaulting" in food webs, in which multiple predator species interact both through their shared resources but also when one predator is able to exploit other predator taxa. Polis (1991) and Polis and Meyers (1989) have developed a similar concept ("intraguild predation," or IGP), describing predators that use similar resources and thus are potential competitors but also prey on each other. Work reviewed by Polis and co-workers indicates that intraguild predation is a nearly ubiquitous component of real food webs; they concluded that food webs in nature are unlikely to conform to the simple configurations originally postulated in the CTI hypothesis. Polis and Holt (1992) suggest that the occurrence of IGP makes the outcome of food web changes considerably less predictable than is suggested by the initial formulations of the CTI hypothesis. Community shifts could compensate for decreases in the abundance of one species, such that the overall intensity of predation on the shared food resources of multiple predator species would be largely unaffected. Few studies at the ecosystem scale have documented how trophic complexity potentially alters the outcome of changes in food web structure on ecosystem processes such as primary productivity.

We investigated the effects and mechanisms of food web alteration on ecosystem processes by manipulating the trophic structure of Castle Lake, California. Recent analyses of the 30-yr data set for Castle Lake have contributed to the accumulating evidence for the role of fish in influencing lake ecosystems (Jassby et al. 1990). Using multivariate techniques for analysis of time series, Jassby et al. isolated two independent components of the spatial (vertical) and seasonal variability in primary productivity (PPr) in this lake. The first and dominant mode of variability involved PPr early in the ice-free season deep in the water column (15–25 m layer); interannual variability in this component was correlated only with climatic variables such as winter precipitation and time of ice-out. The second mode of variability reflected dynamics of PPr in the upper 10 m late in the summer; interannual variation in this mode correlated only with food-web related variables, such as the biomass of the herbivore *Daphnia* (a negative correlation) or the relative abundance of rainbow trout (a positive correlation). To test for the mechanisms underlying these correlations, we initiated a food web manipulation by discontinuing stocking of rainbow trout. Herein we report the dynamics of zooplankton, water transparency, and PPr over a 3-yr period (1989–1991) following stocking manipulation. Dynamics are compared to 3 yr of monitoring before manipulation (1986–1988). We also monitored the dynamics and diets of other potentially planktivorous fish in Castle Lake (brook trout and golden shiners) following the manipulation to evaluate whether compensatory responses among these species influenced the impact of reduced rainbow trout abundance on lower trophic levels.

Methods

Study site and experimental food web manipulation

Castle Lake (mean depth: 11.4 m, maximum depth: 35 m, surface area: 0.21 km^2) is located at an elevation of 1657 m in the Siskiyou mountains of northern California (41°13′ N, 122°22′ W). The lake has been under nearly continuous limnological monitoring since 1959, with an emphasis on nutrient dynamics and primary productivity (Goldman and DeAmezaga 1984). Previous studies have indicated that nitrogen (N) is the nutrient primarily limiting to phytoplankton growth in Castle Lake (Axler et al. 1981, Goldman and DeAmezaga 1984) and so we focus on N dynamics here. The crustacean zooplankton community has generally been dominated by the cladoceran *Daphnia rosea* and the calanoid copepod *Diaptomus novamexicanus,* with *Bosmina longirostris* and *Holopedium gibberum* occurring as subdominants (Janik 1988, Elser 1992). During the period preceding our study, invertebrate predators (e.g., cyclopoid copepods, dipteran larvae) were absent or rare.

As described by Jassby et al. (1990), rainbow trout (*Oncorhyncus mykiss*) and brook trout (*Salvelinus fontinalis*) have dominated the fish community of Castle Lake throughout the 30-yr period of study. Small numbers of golden shiners have been observed since the early 1980s. Brook trout reproduce naturally in Castle Lake (Wurtsbaugh et al. 1975). Rainbow trout do not reproduce in the lake or watershed and are maintained by stocking by the California Department of Fish and Game. Based on prior diet and behavior studies (Swift 1970, Paulson 1977), our own analyses of rainbow trout diets, and the relatively heavy stocking rates, the predominant source of predation pressure on zooplankton in Castle Lake has likely been planktivory by rainbow trout. Creel surveys also indicate that heavy angling pressure removes rainbow trout before they reach sizes at which they would be capable of extensive piscivory (300 mm standard length; Beauchamp 1990). Further support for the suggestion that rainbow trout have functioned predominantly as planktivores in Castle Lake comes from the correlative analyses of Jassby et al. (1990): the secondary mode of PPr variability associated with food web components varied negatively with *Daphnia* biomass but positively with rainbow trout abundance, as gauged by angler catch-per-unit-effort. If rainbow trout exerted their indirect influence on PPr primarily as piscivores (indirectly enhancing *Daphnia*), then this mode of variability should have

varied negatively with rainbow trout abundance. It did not. An alternative explanation for the correlation between productivity variation and trout abundance is that excretion of nutrients by rainbow trout feeding extensively on littoral zone prey items directly affected phytoplankton productivity. Based on previous studies, this possibility appears unlikely. Paulson (1977) compared the nitrogen demand of phytoplankton productivity to estimates of rates of nitrogen excretion by rainbow trout during years of relatively heavy trout stocking (1975–1976). N excretion by rainbow trout only accounted for an average of 3.6% of the growing season N demand, with a maximum summer value of 13%. Thus, it is unlikely that direct effects of trout N excretion were associated with past correlations of PPr variation and trout abundance or with the changes in PPr following stocking manipulation documented in the following.

From 1958 until our experimental manipulations, a nearly constant annual stocking rate of 10 000 underyearling rainbow trout (7–10 cm) had been maintained. These fish were generally added in late summer or early fall. As a result of this external maintenance, rainbow trout have dominated the fishing harvest from the lake, consisting of 75% of the total catch during 1960–1971 and >90% in years of more sporadic creel census in the 1970s and 1980s (Jassby et al. 1990). At our request, California Fish and Game did not stock the lake with rainbow trout in fall 1988; stocking was also withheld during 1989–1990 (stocking was resumed in fall 1991). Thus, the first postmanipulation year for our study was 1989. We monitored limnological dynamics during 1989–1991 and compared these dynamics to the 2- or 3-yr period preceding the manipulation. We also monitored abundance, growth, and diets of fish populations during 1989–1991 to document the decline of rainbow trout due to angling and other mortality and to determine the potential response of naturally reproducing fish planktivores following the reduction of the externally maintained planktivore.

Monitoring

Fish.—Rainbow trout, brook trout, and adult golden shiners were captured in bottom-set gill nets set monthly from June to September in 1989–1991. A stratified random design was used to place one net randomly within each of four areas within the lake each night. Each net was 30 m long, 2 m high, and composed of five mesh sizes (19, 25, 32, 39, and 45 mm bar). Nets were set at night from dusk until dawn; each netting period lasted between two and five nights. All fish were removed from gill nets, measured (total length to the nearest millimetre), weighed (wet mass to the nearest 0.1 g) and sexed. Stomachs of up to 50 individuals of each species were removed and preserved in a 10% formalin solution. Scales of selected rainbow trout and golden shiners were also collected for age determination.

In addition to bottom-set gill nets, a series of vertical gill nets was set at monthly intervals beginning in July 1990. Five nets (3 m wide × 30 m deep, each either 19, 25, 32, 39, or 45 mm mesh) were set at a central lake station for 3–5 d and harvested twice daily at dawn and dusk. The depth of each fish capture was recorded and size and stomach contents were determined.

Stomach contents from gill-netted fish were removed and examined under a dissecting microscope. Prey were assigned to the following categories: daphnids, cyclopoid copepods, calanoid copepods, other zooplankton, crayfish, golden shiners, other fish, aquatic insects, and terrestrial insects. A visual estimate of the volumetric proportion of each group present was made from each stomach. For selected stomachs, the volume of individual prey taxa was measured with a graduated cylinder. The volumetric proportion of prey taxa estimated visually was compared to measured volumetric proportion for these selected stomach contents.

In 1989 only small numbers of age-0 golden shiners were observed in shallow regions of the lake. However, in response to the potential recruitment of golden shiners to the pelagic zone, in 1990 we began small-fish sampling using modified acoustic surveys and purse seines. Juvenile golden shiners were collected in the pelagic zone with a small purse seine (34 m long × 9 m deep, 3.2 mm mesh). The purse seine was set at 4–6 locations during the day (1200–1600) and night (2200–0100) in the pelagic region on several dates in July and August of each year. The net sampled a volume of ≈380 m^3 and fished efficiently from the surface to a depth of 5 m. Golden shiners were the only fish species captured. Each individual was measured (total length ± 0.1 mm), weighed (wet mass ± 0.01 g), and preserved in 70% EtOH for examination of stomach contents. Each item was identified as daphnid, cyclopoid copepod, calanoid copepod, copepod nauplii, aquatic insect, or terrestrial insect and measured to the nearest 0.03 mm with a dissecting microscope.

A series of hydroacoustic surveys was conducted in early September of each year to assess the abundance and spatial distribution of fish. One survey consisted of six cross-lake transects covering a distance of 3.2 km. Preliminary surveys indicated that fish densities were highest from midday until dusk; therefore we focused our acoustic sampling on this period. Each survey was repeated twice during the day (1300–1500) and twice during dusk periods (beginning 1 h after sundown). Acoustic surveys were then repeated the next day providing four estimates during the day and four estimates from the dusk period. Acoustic studies were made with a BioSonics model 105 echosounder equipped with a 420-kHz dual beam (6 × 15°) transducer (BioSonics, Seattle, Washington, USA) that permitted estimates of fish size. We sampled at a rate of 2 pings/s traveling at a boat speed of 2–4 m/s. Data were recorded directly into computer files as digitized

echoes and were also digitized and recorded on Betamax videotape.

Along with the moving acoustic surveys, beginning in 1990 we also collected acoustic data from a stationary platform near the middle of the lake to estimate abundances of golden shiners that primarily occupied surface layers poorly sampled by moving acoustic surveys. For these stationary surveys we submerged the transducer to a depth of 2 m and pointed the acoustic beam sideways so that a large volume of epilimnetic water within 90 m of the transducer was being sampled. These stationary surveys were conducted just before nighttime purse seine collections. Each survey consisted of four 15-min periods of data collection with the transducer set from a different side of the platform.

Acoustic data were analyzed by counting echoes with dual beam information processed with a BioSonics ESP Dual Beam Processor (Model 281) and software (BioSonics, Seattle, Washington, USA). Only single fish targets within 4° of the acoustic beam axis were used to calculate fish target strength and to obtain fish density estimates. Stationary surveys were assumed to primarily sample golden shiners while roving surveys were assumed to sample trout populations (after correction for small targets). We used single fish targets with dual beam target strengths ranging from −59 to −35 decibels (db), representing fish of ≈1–40 cm total length (TL) (Love 1971). Fish targets between −52 to −35 correspond to salmonids greater than 1 year of age or to adult golden shiners (5–40 cm). Fish targets between −59 and −52 db correspond to young-of-year golden shiners or brook trout of 1–5 cm TL. Only echoes that met the single-target shape criteria used by the analysis software were selected to calculate densities and target strengths. The bottom window region where fish targets were indistinguishable from the bottom was set at 1.0 m.

Limnological parameters.—Most of the methods for monitoring of physical, chemical, and biological characteristics of Castle Lake have been held constant throughout the 30 yr that the lake has been studied. Details can be found in previous publications (Goldman and DeAmezaga 1984, Goldman et al. 1989, Jassby et al. 1990). The lake was sampled at a single station in the deepest part of the lake at 5-d (1986–1988) or 7-d (1989–1991) intervals during the summer (June–September). In other months, sampling frequency was similar (for example, the periods following ice-out in 1990–1991) or less frequent (2–3 wk intervals in fall and spring, monthly intervals in winter, depending on the condition of the ice cover). On each date, vertical profiles of temperature (at 1-m intervals using a thermistor), dissolved chemical nutrients (NO_3-N and NH_4-N; 3–5 m depth intervals), and primary productivity (PPr; 1–3 m intervals) were determined. Water transparency was quantified by measuring the vertical profile of light penetration (photosynthetically active radiation) from 0 to 30 m using a submersible quantum sensor and by using a 20-cm white Secchi disk. Water chemistry analyses were usually performed on fresh filtered samples. NO_3-N was determined using the hydrazine reduction method (Kamphake et al. 1967) and NH_4-N by the phenol-hypochlorite method (Solorzano 1969). Concentrations of soluble reactive phosphorus were also determined but concentrations were extremely low and erratic and will not be presented. PPr was determined using the ^{14}C method (Goldman 1968) with 4-h incubations performed in situ during the midday. Concentrations of dissolved inorganic carbon were determined using an infrared analyzer. After incubation in the presence of 74–185 kBq of $NaH^{14}CO_3$, phytoplankton were filtered onto Millipore type HA membrane filters (0.45-μm pore size), dried, and assayed for radioactivity using a thin-window Geiger-Mueller counter. Further details regarding methods for PPr estimates may be found in Goldman (1968) and Goldman and DeAmezaga (1984).

Because the mode of variability most strongly correlated with food web dynamics in the analyses of Jassby et al. (1990) occurs in the surface waters, we decided to streamline zooplankton collections by obtaining composite samples from the epilimnion (generally 0.5, 3, and 5 m) rather than discrete samples from multiple depths throughout the water column. This approach was initiated in 1987 and therefore we present no zooplankton data for 1986. Zooplankton samples were collected using a 12-L clear Schindler sampler. Because zooplankton in Castle Lake engage in pronounced diel vertical migration (Redfield and Goldman 1978), we sampled both during the day (1100–1300 Pacific Standard Time [PST]) and at night (2000–0000 PST) so that on each date two epilimnetic composite samples were obtained. During our study period, two mesh sizes (64 μm, 1987–1989; and 85-μm, 1990–1991) were used in collection nets in the Schindler sampler. Examination of samples collected with both meshes indicated that samples obtained with 85-μm mesh considerably underestimated rotifers and nauplii. As we have been unable to establish a reliable correction factor for this effect, we report results for crustacean zooplankton taxa only (excluding nauplii).

Zooplankton samples from 1987 to 1988 were preserved in ≈5% sucrose-formalin; samples from 1989–1991 were preserved with Lugol's solution buffered with sucrose. Samples were examined under a dissecting microscope and enumerated according to species. Biomasses of crustacean zooplankton were estimated using standard length-mass regressions (Downing and Rigler 1986) or relationships developed specifically for certain Castle Lake taxa (Redfield 1980), allowing us to estimate total zooplankton biomass on each sampling date as well as the biomass contributed by the major crustacean species.

Data analyses

Fish consumption dynamics.—We used a bioenergetics analysis of fish growth processes (Hewett and

Johnson 1987) to estimate the seasonal and annual consumption dynamics of fish populations in Castle Lake from 1989 to 1991. These energy simulations allow estimation of consumption of different prey types by the average individual of a fish cohort given information on growth rate, diet proportions, and thermal history of individual fish of that cohort. The simulation model operates by iteratively fitting an average consumption rate (*P* value) such that the observed growth of the mean individual fish of a cohort is realized. The *P* value is expressed as a proportion of the maximum consumption possible for a fish of a given size and species, at the prescribed temperature. These estimates of individual consumption were then multiplied by the abundance of fish in each cohort to determine the consumption dynamics of each fish population. We used Hewett and Johnson's (1987) generalized salmonid parameters for analysis of rainbow trout and brook trout, and their generalized cyprinid parameters for golden shiner. This approach allowed us to examine the effects of concurrent changes in abundances of planktivorous fish species and their diet compositions on overall rates of vertebrate predation on zooplankton populations (Luecke et al. 1990*a*, 1992, Stewart and Iberra 1991). We stress interannual changes in consumption of *Daphnia* as this prey item was the most frequently eaten zooplankton species taken by all three fish species. We also emphasize that, while aquatic and terrestrial insects comprised a substantial proportion of the diets of all three species, the relevant parameter from our perspective was primarily whether rates of vertebrate planktivory on *Daphnia* were important for *Daphnia* dynamics rather than whether *Daphnia* was the dominant food source for the fish.

Information on growth rate and diet proportion came from fish captured in gill nets and purse seines. Thermal history was derived from the location of salmonids in vertical gill nets, the depth of hydroacoustic targets, and weekly vertical temperature profiles. Abundance estimates of salmonids were derived from acoustic sampling of fish targets proportioned into species and cohorts based on gill net catches. Golden shiner abundances were estimated from hydroacoustic surveys and purse seine catches.

A repeated-measures ANOVA was used to test for interannual differences in gill net catches; catch-per-unit-effort in each summer month was the repeated variable. The statistical significance of interannual differences in fish density determined by hydroacoustics was determined by ANOVA.

Limnological parameters.—To characterize the seasonal development of water column stratification, we calculated Schmidt stability (S; Schmidt 1928) based on the lake's hypsographic curve and the temperature profile. S is an integrated measure of the amount of work that would be required to completely homogenize the water column of the lake given its temperature (density) distribution on a given date. S provides an index of the interannual and intra-annual dynamics of physical variation due to changes in insolation, wind, and air temperature. Water density was calculated as a function of temperature and depth using the International Equation of State (Millero and Poisson 1981).

Many of our analyses focused on the dynamics of parameters in the epilimnion as variability in the seasonal development of primary productivity in the epilimnion correlated most strongly with food web parameters in the study of Jassby et al. (1990). We calculated mean concentrations of NO_3-N and NH_4-N in the surface waters (usually 0, 3, and 5 m) to evaluate changes in the availability of nitrogen during the study period. We also segregated our analyses of the PPr data into considerations of: (1) whole water column data; (2) data confined to the upper 10 m to specifically examine changes in productivity in the layer identified by Jassby et al. (1990) as most correlated with food web variables; and (3) data confined to the 15–25 m layer identified by Jassby et al. (1990) as correlated with climatic variables. We were also interested in examining changes in the seasonality of various parameters, especially in the abundance and composition of the zooplankton and in phytoplankton productivity. To do this, we generally aggregated data within 2-wk intervals for the summer period (June–September) and examined intra-annual dynamics in different years. By aggregating data within 2-wk intervals and using only the means within those intervals in our analyses, potential effects of differential sampling intensity during different years or months were minimized.

Approaches to the interpretation of the results of whole-ecosystem perturbations have been the subject of considerable debate (Hurlbert 1984, Stewart-Oaten et al. 1986, Carpenter 1990). The results reported here examine temporal dynamics during 3-yr intervals before and after a deliberate perturbation of a single system. Thus, we cannot employ the BACI approach described by Stewart-Oaten et al. (1986) or Randomized Intervention Analysis (RIA) for paired experimental-reference systems as developed by Carpenter et al. (1989), as these approaches require simultaneous sampling of a paired reference system. In this paper we apply a hybrid approach. First, we follow the recommendations of Hurlbert (1984) and present graphical summaries of responses, along with response variability, permitting a direct evaluation of the magnitude of imputed changes in various variables. Our interpretations are enhanced by our access to a long record of monitoring for this ecosystem and thus we can better evaluate whether conditions following manipulation are anomalous. Second, we were interested in examining whether response variables changed both on interannual and intra-annual (i.e., seasonal) time scales following stocking manipulations. To do so, we employed repeated-measures (RM) ANOVA (Gurevitch and Chester 1986) comparing premanipulation (1986–1988) and postmanipulation (1989–1991) periods using

data segregated into 2-wk intervals, testing for significant "period" (i.e., pre- vs. postmanipulation) × sampling interval (i.e., seasonal development) interaction terms. This analysis also permits conservative univariate tests of "main effect" differences between pre- and postmanipulation periods while compensating for sequential correlation for observations made within years. Because RM ANOVA does not compensate for potential sequential correlation of observations between different years within the pre- and postmanipulation periods we also tested for differences between pre- and postmanipulation periods using Randomized Intervention Analysis, with correction for lag-1 autocorrelation (Carpenter et al. 1989). Results for RM ANOVA and RIA regarding statistical significance of pre- and postmanipulation changes were generally consistent and so we do not present RIA results here. It is important to note that significant differences between pre- and postmanipulation periods, whether detected by RM ANOVA or RIA, do not necessarily demonstrate a causal relationship between the manipulation and the response variable. As discussed by Carpenter (1990), conclusions regarding causality ultimately rest on the soundness of the biological reasoning that accompanies the analysis.

Results

Physical–chemical conditions

Castle Lake experienced an irregularly variable climatic regime during the 6-yr study period, resulting in some degree of interannual variability in water column stability (Fig. 1A) and the timing of physical events such as ice break-up. Ice break-up occurred as early as day 93 of the year (early April) in 1990 and as late as days 139–142 (mid-May) in 1988 and 1991. In contrast to the 49-d difference for the time of ice-out, the date on which maximum water column stability occurred varied by only 21 d. This narrow range in the timing of peak stability indicates that water column conditions late in the stratified season are relatively insensitive to the fine-scale details of climate that determine the timing of ice-out and initial thermal stratification. Therefore, comparison of summer limnological dynamics on a calendar-year basis, as done by Jassby et al. (1990), is valid. No substantial differences between pre- and postmanipulation years were observed for S that might obscure evaluation of the impacts of food web manipulations on this system (Fig. 1A; RM ANOVA: $F_{1,4} = 3.76$, $P = 0.13$).

NO_3-N and NH_4-N were highly variable during the study period, both within and between years (Fig. 1B, C). High concentrations of nutrients accumulated under the ice and were rapidly depleted following ice-out. NH_4-N was particularly variable and no seasonal or manipulation period differences were observed. NO_3-N varied seasonally (RM ANOVA: $F_{7,28} = 7.26$, $P < 0.001$). NO_3-N seasonality differed between pre- and postmanipulation periods (RM ANOVA: $F_{7,28} = 5.57$, $P < 0.001$), reflecting a tendency in postmanipulation years (especially 1990 and 1991) for NO_3-N concentrations to be relatively low and constant for all four summer months while in premanipulation years NO_3-N in June was relatively high. Most importantly for interpretation of increases in PPr and decreases in water clarity following the manipulation, these data indicate that major abiotically driven differences in nutrient loading coincident with the food web manipulation did not occur.

Fish sampling

Rainbow trout catches in standardized horizontal gill nets decreased from 1989 to 1991 (Fig. 2). Rainbow trout CPE (catch per effort) was significantly different among years (RM ANOVA: $F_{2,6} = 105.6$, $P < 0.001$). A Bonferroni multiple comparison of means indicated that catch rates declined significantly each year of the study. During this period, brook trout catches increased (Fig. 2; RM ANOVA: $F_{2,6} = 53.9$, $P < 0.001$). Based on a Bonferroni comparison of means, brook trout catches were lower in 1989 than in 1990 and 1991.

The abundance of golden shiners also increased from 1989 to 1991. In 1989 a few adult golden shiners were captured in horizontal gill nets, but no young-of-the-year (YOY) golden shiners were observed in the main basin of the lake. In June 1990 a small number of golden shiners were again captured in gill nets, and numerous YOY golden shiners were observed in the pelagic regions of the lake. Purse seine catches and stationary epilimnetic hydroacoustic sampling indicated that the golden shiner population produced two very strong year classes in 1990 and 1991 (Table 1).

Brook trout and golden shiner populations appeared to compensate for reduced rainbow trout abundance, as hydroacoustic estimates of total pelagic fish abundance were similar among years (Fig. 3; ANOVA of density of fish targets larger than −52 db (5 cm TL): $F_{2,10} = 0.122$, $P = 0.74$). Gill net catches indicated that the reduction in rainbow trout numbers was primarily compensated for by increases in brook trout.

In addition to changes in the abundance of fish species in Castle Lake, the size distributions of these populations also changed between 1989 and 1991. The majority of rainbow trout sampled during this study resulted from fish stocked in fall 1987 and spring 1988, as there was no indication of natural reproduction in the lake. Mean length of rainbow trout captured in gill nets increased from 244 mm in 1989 to 281 mm in 1991 as this 1988 cohort grew in size. The mean length of brook trout captured in gill nets decreased as this species produced relatively stronger year classes after stocking of rainbow trout ceased. The two very strong year classes of golden shiners produced in 1990 and 1991 resulted in a decrease in the mean length of shiners collected in gill nets from 135 mm in 1989 to 86

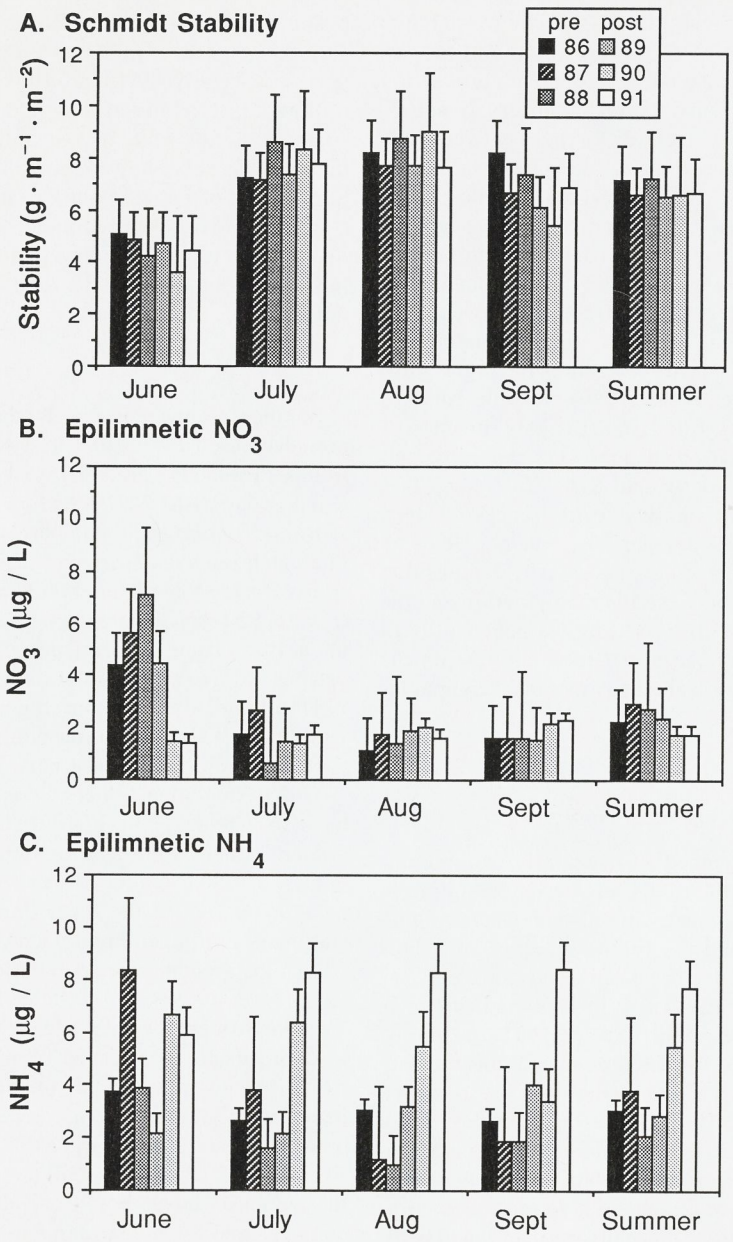

FIG. 1. Dynamics of monthly mean and summer mean values of: (A) water column stability, (B) epilimnetic NO_3-N, and (C) epilimnetic NH_4-N, in Castle Lake during during 1986–1991. Monitoring data were first segregated into two intervals per month and the mean of all observations within that interval was calculated. Error bars indicate 1 SD calculated for those duplicate values per month or for the eight observations for the summer season.

mm in 1991. Shiners captured in purse seines in August of 1990 and 1991 averaged 36 and 43 mm, respectively.

These changes in abundances and size distributions of fish populations resulted in changes in total and relative species biomass in the fish assemblage of Castle Lake (Fig. 4). Total fish biomass was lowest in 1990 but increased to the highest levels in 1991 due mainly to increases in age-2 brook trout.

Diet analyses of the three species of planktivorous fish indicated that *Daphnia* comprised a higher proportion of stomach contents of golden shiners than of rainbow or brook trout (Fig. 5). A substantial proportion of the diets of the salmonids consisted of terrestrial and aquatic insects. Daphnids comprised a higher proportion of the diet of rainbow and brook trout in late summer compared to other seasons as high surface water temperatures likely precluded salmonids from rising to the surface to consume terrestrial insects. During

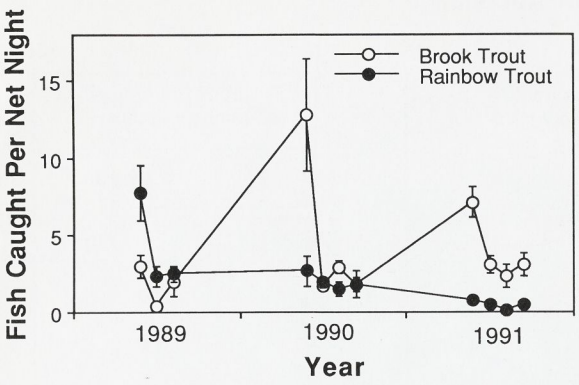

FIG. 2. Catch-per-unit-effort of rainbow and brook trout in 1989–1991. Data represent means (±1 SE) of number of fish caught in four nets set per night (2–5 consecutive nights of sampling per sampling event). Nets were set in June, July, and August of 1989 and in June, July, August, and September of 1990 and 1991.

late summer, ≈25% of salmonids and 65% of golden shiner diets were composed of daphnids (Fig. 5). In 1991, however, the few remaining, relatively large rainbow trout (mean length 321 mm) did not consume zooplankton. Few other zooplankton taxa were present in fish stomachs.

Consumption dynamics of fish

Bioenergetics simulations were conducted to estimate how changes in the fish assemblage affected rates of fish consumption of zooplankton species among years. Inputs to the energy simulations are presented in Table 2 and Fig. 5. Changes in masses of each cohort of fish (Table 2) were low compared to other populations (Tabor and Wurtsbaugh 1991). Abundance estimates for each cohort were estimated from August acoustic and purse seine sampling (Table 2). We assumed that these abundances were representative of midsummer conditions. Results of energy simulations indicated that consumption of daphnids was greatest in mid- to late summer of each year (Fig. 6). In 1989 rainbow trout consumed the greatest mass of daphnids, followed by brook trout and golden shiners. Rainbow trout consumption of daphnids declined during the 3-yr period as abundance of this fish dwindled and the remaining larger rainbow trout consumed fewer daphnids. However, late summer consumption of daphnids by the total fish assemblage was three times as great in 1991 compared to 1989. This increase occurred mostly because of greater numbers of brook trout and golden shiners that consumed higher proportions of daphnids than rainbow trout (Fig. 5). The higher mass-specific consumption demand of the smaller brook trout and golden shiners also contributed to increased estimates of total predation on daphnids.

Zooplankton

The first and most pronounced change in the zooplankton community following cessation of rainbow trout stocking in fall 1988 was a dramatic increase in early 1989 in the abundance of the planktivorous cyclopoid copepod *Diacyclops thomasi* (Fig. 7A). This species was present only at background densities during 1987 and 1988, as well as during nearly 20 yr for which zooplankton data are available, but reached densities of 10 animals/L (average of day and night samples) early in 1989 and increased more in 1990 and 1991, peaking at 25 animals/L in midsummer 1990. The absence of appreciable densities of *D. thomasi* from nearly 20 yr of zooplankton collections in Castle Lake argues strongly that the increase observed in 1989 was highly unusual. Although potentially superfluous for such a dramatic event, statistical tests of differences in densities of *D. thomasi* in years before and after the manipulation were significant (RM ANOVA $F_{1,3}$ = 26.6, P = 0.014). Accompanying this increase in *D. thomasi* in 1989 was a decline in the biomass of the herbivorous calanoid copepod *Diaptomus novamexicanus* that began in midsummer 1989 (Fig. 7B). The decline in *D. novamexicanus* following manipulation was marginally significant (RM ANOVA: $F_{1,3}$ = 6.12, P = 0.089).

The epilimnetic biomass of *Daphnia rosea* in 1989 was similar to 1987 and 1988 (Fig. 7C); however, *Daphnia* biomass decreased substantially in 1990 and 1991. These declines were particularly pronounced late in the summer, as *Daphnia* declined precipitously during these months in postmanipulation years but remained high during this period in the previous 3 yr. Reflecting the apparently delayed response of *Daphnia* to trout manipulation, *Daphnia* biomass in pre- and postmanipulation periods did not differ significantly (RM ANOVA: $F_{1,3}$ = 0.70, P = 0.46). However, there was a significant seasonal trend in *Daphnia* biomass (RM ANOVA: $F_{5,15}$ = 3.96, P = 0.017) and a signif-

TABLE 1. Density (numbers per 1000 m^3) and lake-wide abundance of golden shiners in the epilimnion during late August of 1990 and 1991. Mean (± 1 SE) of density of small fish targets (−59 to −52 db) in four side scanning hydroacoustic samples, and mean (± 1 SE) of eight purse seine estimates are presented. Estimates were based on nighttime assessments only; densities of fish estimated from nighttime purse seine and acoustic surveys were 10 and 4 times higher, respectively, than daytime estimates. Abundances were calculated assuming these densities included only the top 5 m of the lake. Due to low abundances, no efforts were made to quantify golden shiner densities in 1989.

	1990	1991
Acoustic density ($\bar{X}$ ± 1 SE)	6.98 ± 1.29	9.72 ± 2.47
Purse seine density ($\bar{X}$ ± 1 SE)	7.46 ± 2.88	6.13 ± 3.45
Acoustic abundance	7540	10 500

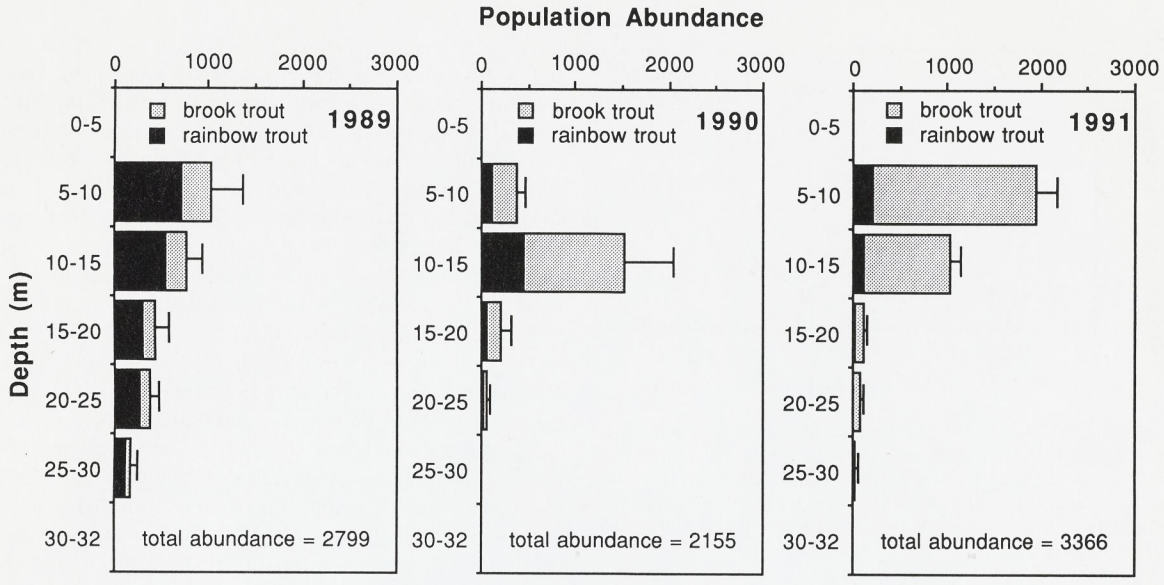

FIG. 3. Hydroacoustic estimates of pelagic fish abundance in 1989–1991. Mean estimates (and 1 SE) of fish abundance stratified by depth from four surveys collected on two nights in late August or early September of each year are depicted. Abundances were calculated from the product of densities and volume of water in each depth strata. Hydroacoustic targets were partitioned into rainbow (black) and brook trout (stippled) based on relative catch in gill nets. Lake-wide estimates of fish populations are indicated.

icant change in this seasonality before and after the manipulation (RM ANOVA: $F_{5,15} = 3.63$, $P = 0.024$), reflecting the tendency for *Daphnia* biomass to increase during summer months before the manipulation but to decrease during summer following the manipulation (Fig. 7C).

Dynamics of subdominant taxa (*Holopedium, Bosmina*) were somewhat erratic and more difficult to interpret. *Bosmina* and *Holopedium* biomass generally appeared to increase following manipulation (Fig. 7E, F); however, these changes were not statistically significant (RM ANOVA: $F_{1,3} < 4.02$, $P > 0.13$).

Total herbivorous crustacean biomass (excludes *D. thomasi*) appeared to decline during the postmanipulation period (Fig. 7F). During 1990 and 1991, average September herbivore biomass was 58 and 43% of its levels, respectively, in 1987–1988. Average summer herbivore biomass was relatively unchanged in 1989 compared to 1987–1988 but was reduced in 1990 to 67% and in 1991 to 36% of premanipulation levels. Despite the sizable reductions in 1990 and 1991, pre- and postmanipulation periods did not differ statistically in total herbivore biomass (RM ANOVA: $F_{1,3} = 0.48$, $P = 0.54$), likely the result of both the delay in the *Daphnia* reduction following the manipulation as well as partially compensating reciprocal responses in *Bosmina* and *Holopedium* (Fig. 7D, E).

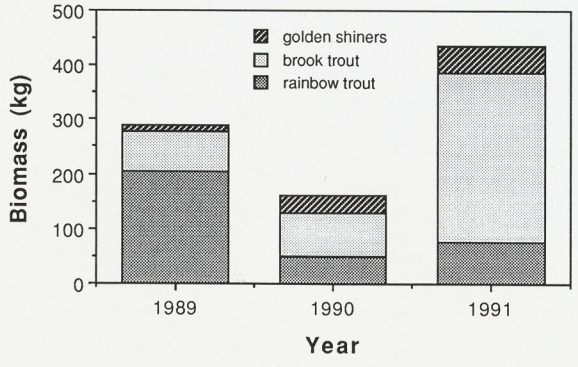

FIG. 4. Biomass of fish species in 1989–1991 estimated from abundances of fish sampled with mobile and side-scan acoustic surveys multiplied by the mean mass of individuals collected in gill net and purse seine samples from each year.

Productivity and water clarity

Phytoplankton-related ecosystem responses to the changing food web were examined by considering two main parameters: primary productivity and water transparency. We considered two aspects of PPr: whole water column values and the amount of PPr in the 0–10 m layer (shallow) vs. in the 15–25 m layer (deep). We examined three measures of water transparency: Secchi depth (which in Castle Lake characterizes light penetration through both the epilimnion and much of the metalimnion), the depth of 1% light penetration (euphotic zone depth), and the vertical attenuation coefficient (k per metre) for photosynthetically active radiation in the 0–10 and 15–25 m water layers. In Castle Lake, as in most unstained lakes, water transparency and light penetration are determined primarily by the

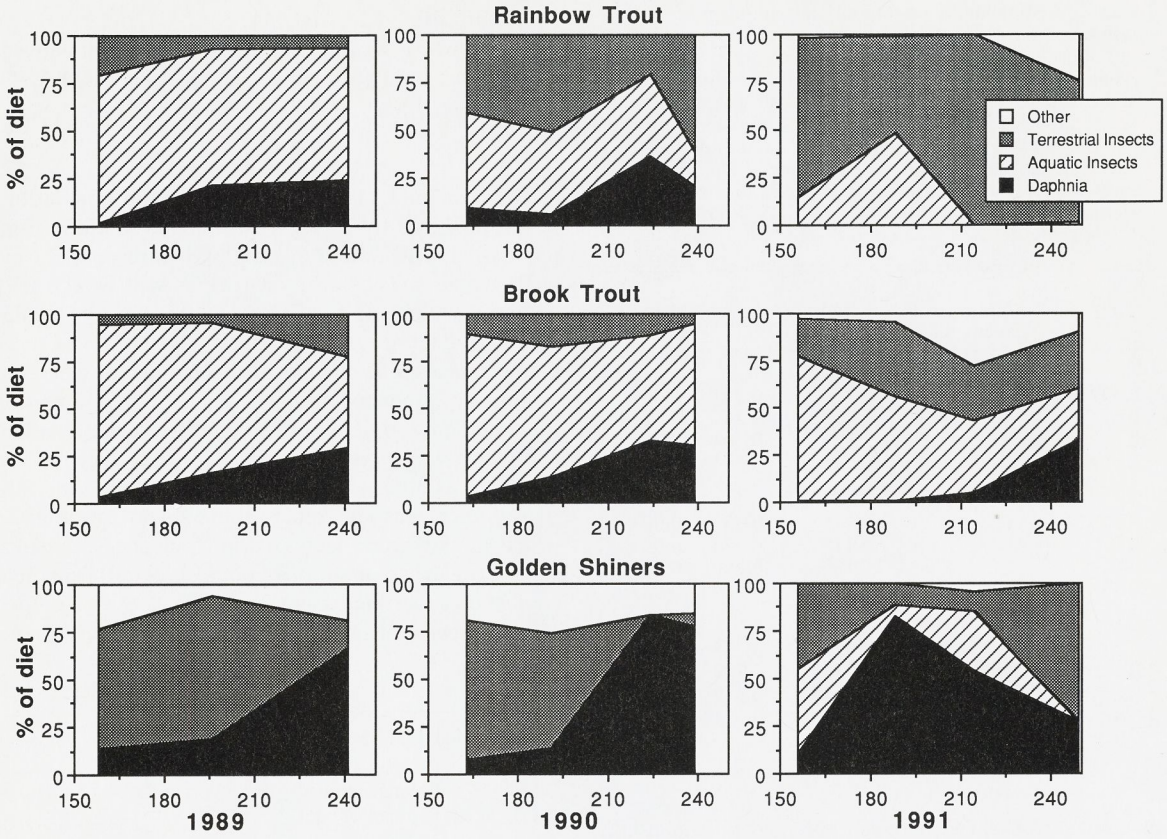

FIG. 5. Percent composition of diet of rainbow trout, brook trout, and golden shiners as determined volumetrically from stomach samples taken from fish collected in gill nets during summers of 1989–1991. "Other" prey include nondaphnid zooplankton, chydorids, and molluscs.

total concentration of phytoplankton and detritus (Priscu 1983, Elser 1988). A secondary but substantial influence is associated with the size distribution of phytoplankton cells, as small cells are more efficient in absorbing and scattering light for a fixed total biomass (Elser 1988, Mazumder et al. 1990). Thus, the decreases in water clarity that we report here potentially reflect increases in both the abundance of suspended particles and in the relative contribution of small phytoplankton taxa.

Secchi transparency declined rapidly in 1989 compared to premanipulation levels, with decreases in water transparency observed as early as July of that year (Fig. 8A; RM ANOVA: $F_{1,4} = 76.2$, $P < 0.001$). Reductions in water clarity appeared to be strongest in late summer (August/September). The unusual nature of the decline in late summer Secchi transparency from ≈12–13 m in 1986–1988 to 9–10.5 m in 1989–1991 can be better appreciated by considering the long-term dynamics of this parameter in Castle Lake (Fig. 9). Late summer Secchi transparency values as low as those seen during each of the 3 yr between 1989 and 1991 have been observed on only one occasion (1981) in the 17-yr data record, with 1984 transparency being nearly as low. No sustained (≥3-yr) period in the data record of water transparency was observed as low as that in the 3 yr following food web manipulation.

Responses of light penetration parameters were similar to those observed for Secchi transparency. Euphotic zone depth declined in the postmanipulation period from average summer values of ≈23–25 m in 1986–1988 to ≈19–20 m in 1989–1991 (Fig. 8B; RM ANOVA: $F_{1,4} = 28.2$, $P = 0.006$). Effects of manipulation on euphotic zone depth appeared to occur even more rapidly than for Secchi depth, with reductions in euphotic zone depth apparent in June 1989. Decreases in water clarity occurred throughout the water column, as light extinction in both shallow (0–10 m) and deep (15–25 m) layers increased (RM ANOVA: $F_{1,4} > 13.2$, $P < 0.03$).

While changes in water transparency following food web manipulation were immediate and strong, changes in ecosystem productivity patterns were more subtle (Fig. 10). Pre- and postmanipulation levels of water column and layer-specific PPr were more variable than water transparency parameters, including relatively high PPr values in 1988 and relatively low values in 1991. As a result, only marginally significant differ-

TABLE 2. Abundance, beginning and ending masses, mortality, and the proportion of maximum consumption (P value) of each cohort of fish used in bioenergetics simulations. Abundance estimates were calculated from hydroacoustic surveys partitioned to species based on gill net or purse seine catches. Beginning and ending masses were from early June and early September for salmonids and early July and late August for golden shiners. Daily mortality rates were estimated from annual losses of a cohort. RBT = rainbow trout, BT = brook trout, GS = golden shiner. "2^+" refers to the age-2 cohort.

	Abundance	Beginning mass (g)	Ending mass (g)	P	Mortality (d^{-1})
1989					
RBT 2^+	1230	109	134	0.341	0.001
RBT 3^+	752	154	190	0.347	0.001
BT 3^+	817	142	166	0.401	0.001
GS $\geq 2^+$	347	8.7	15	0.541	0.00175
1990					
RBT 3^+	621	179	215	0.337	0.001
BT 2^+	1023	68	119	0.374	0.001
BT 3^+	511	100	135	0.590	0.001
GS 0^+	7540	0.02	0.54	0.587	0.023
1991					
RBT 4^+	335	197	214	0.238	0.001
BT 2^+	2180	69	111	0.374	0.001
BT 3^+	851	121	144	0.312	0.001
GS 0^+	6980	0.03	0.61	0.621	0.023
GS 1^+	3620	1.32	8.40	0.695	0.0036

ences were observed between pre- and postmanipulation periods for water column PPr (RM ANOVA: $F_{1,4} = 4.88$, $P = 0.09$) and shallow PPr (RM ANOVA: $F_{1,4} = 6.12$, $P = 0.068$). The manipulation appeared to affect PPr more strongly in the surface layer (0–10 m) relative to deep water (15–25 m) (Fig. 10B, C) as RM ANOVA did not detect even marginally significant differences for deep water PPr (RM ANOVA: $F_{1,4} = 0.86$, $P = 0.41$). In contrast to small pre- and postmanipulation differences in PPr on interannual time scales, pre- and postmanipulation periods differed considerably in the intra-annual (seasonal) development of PPr (Fig. 10). PPr for both shallow and deep water layers was strongly seasonal (RM ANOVA: $F_{7,28} > 3.44$, $P < 0.01$). In the shallow layer, PPr increased during the June–September period during premanipulation years but, following the manipulation, generally remained unchanged during the summer season (Fig. 10B). This shift in seasonal development following manipulation was statistically significant (RM ANOVA: $F_{7,28} = 2.42$, $P = 0.045$). In contrast, PPr in the deep layer generally decreased during the summer prior to the manipulation but increased or was largely unchanged following the manipulation (Fig. 10C). This shift in seasonal development following manipulation was also statistically significant (RM ANOVA: $F_{7,28} = 2.89$, $P = 0.021$). Because both seasonal and pre- vs. postmanipulation shifts in PPr in shallow and deep water layers had opposite tendenciés, total water column PPr (the sum of PPr in deep and shallow layers) was not strongly seasonal (Fig. 10A; RM ANOVA: $F_{7,28} = 1.26$, $P = 0.31$), but there was a significant change in seasonal patterns between pre- and postmanipulation periods (RM ANOVA: $F_{7,28} = 2.81$, $P = 0.024$).

DISCUSSION

The dynamics of fish and zooplankton populations in Castle Lake following cessation of rainbow trout populations illustrate the complex nature of real food webs where species prey on species with which they potentially compete for resources. As density of rainbow trout declined, factors governing survival of small fishes appeared to change in that golden shiners and brook trout produced strong year classes. Competition for common zooplankton resources, direct predation, and changes in perceived risk of predators can all be proposed as alternative hypotheses to explain the observed increases in golden shiners and brook trout when rainbow trout decreased in abundance. Evidence supporting the competition hypothesis comes from field enclosure experiments conducted in 1992, in which shiner growth rate was strongly and positively corre-

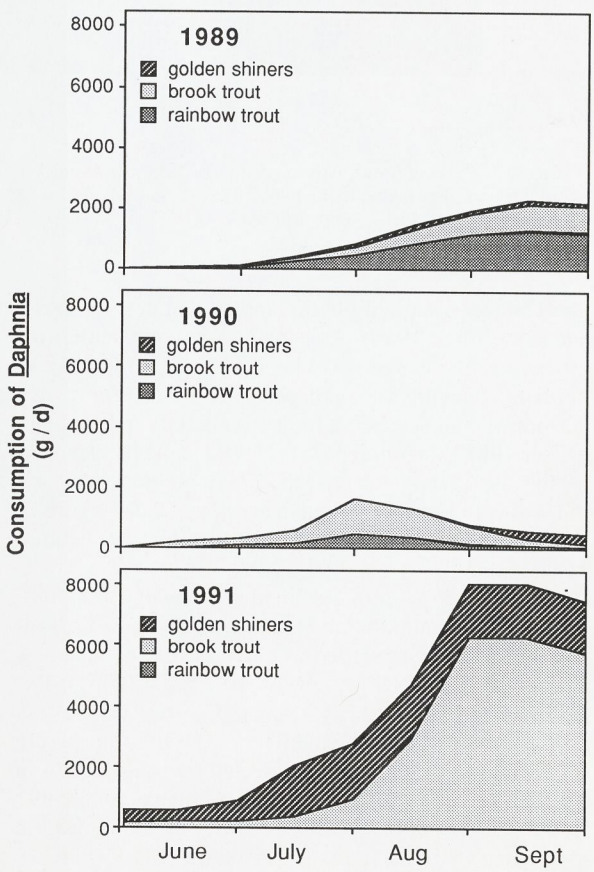

FIG. 6. Consumption of *Daphnia* estimated using bioenergetics simulations for 1989–1991. Rainbow trout were present in 1991 but diet analysis indicated that they did not consume *Daphnia*.

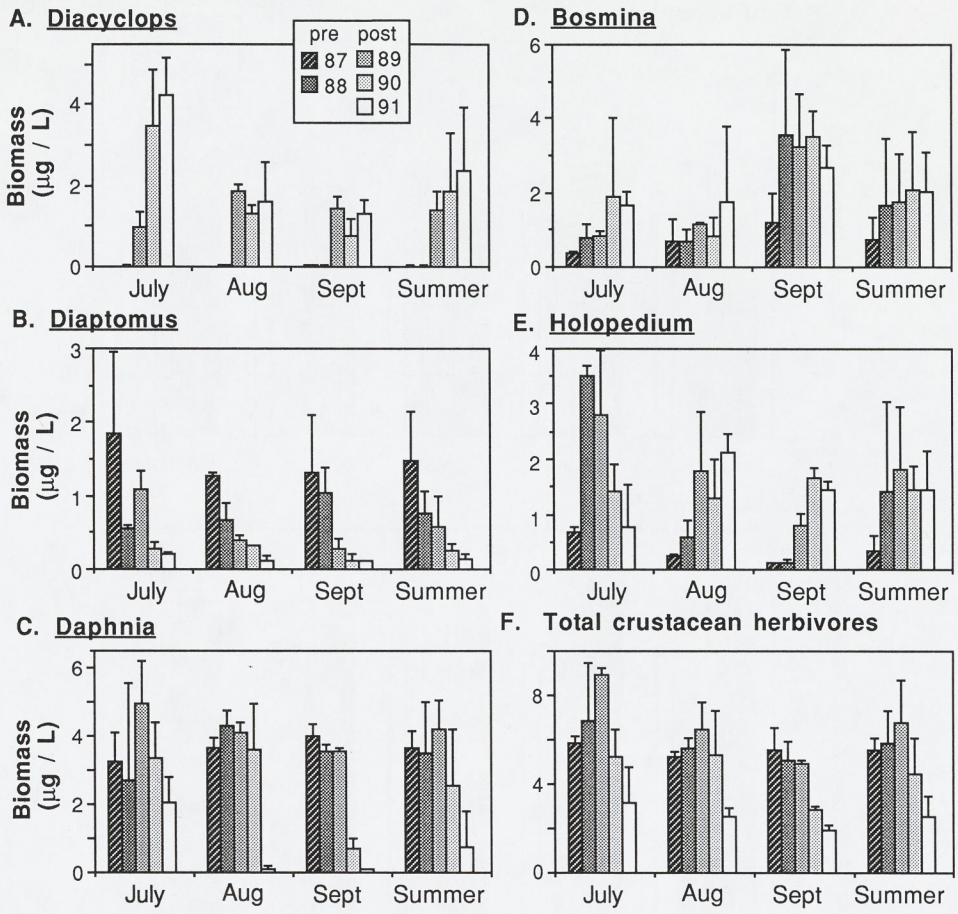

FIG. 7. As in Fig. 1, but for average day-night epilimnetic dry biomass of: (A) the cyclopoid copepod *Diacyclops thomasi,* (B) the calanoid copepod *Diaptomus novamexicanus,* (C) *Daphnia rosea,* (D) *Bosmina longirostris,* (E) *Holopedium gibberum,* (F) all crustacean herbivores (excludes *D. thomasi*). Zooplankton data were not available for 1986.

lated with *Daphnia* biomass (Brandt 1994). Although golden shiners can likely feed more efficiently on zooplankton than can rainbow trout, the consumption of *Daphnia* by this artificially maintained planktivore may still have reduced shiner growth. We have little evidence supporting the predation hypothesis. While large rainbow trout can feed on small cyprinids (Beauchamp 1990), we identified only six golden shiners in the stomach contents of over 400 rainbow trout collected from 1989 to 1992. Relevant to the predation risk hypothesis, growth of cyprinids is often reduced in the presence of piscivores (Gilliam et al. 1989, He and Kitchell 1990, Mathis and Smith 1992). In our study, golden shiners made extensive use of the food-rich pelagic regions only at night when risk of encountering piscivorous trout was low (Brandt 1994). In further support of the predation risk hypothesis, golden shiner growth rates were reduced when either visual or olfactory cues of rainbow trout were present in swimming pool experiments (C. Luecke, *unpublished data*). On the basis of this evidence we conclude that the dramatic increase in abundances of brook trout and golden shiners after rainbow trout densities declined occurred as a result of the combined effects of perceived predation risk and competition for shared zooplankton resources.

The pronounced effect of rainbow trout on the fish assemblage of Castle Lake may reflect the artificial maintenance of rainbow trout by sustained stocking prior to 1989. These individuals, when stocked into the lake as small juveniles, are likely past the stage in their life history when recruitment is most variable (Sissenwine 1984) and recruitment success is determined (Miller et al. 1988). Populations that are artificially maintained, such as the rainbow trout of Castle Lake, have been described as donor-controlled components of the ecosystem (Vadas 1989). Donor control of certain ecosystem components can lead to greater stability and less variation in other ecosystem components. The relatively constant stocking rate of rainbow trout into Castle Lake before 1989 thus may have been responsible for the relatively small contribution of consumer effects to explanations of variation in primary production in the time series analyses of Jassby et al. (1990).

The artificial nature of the maintenance of rainbow

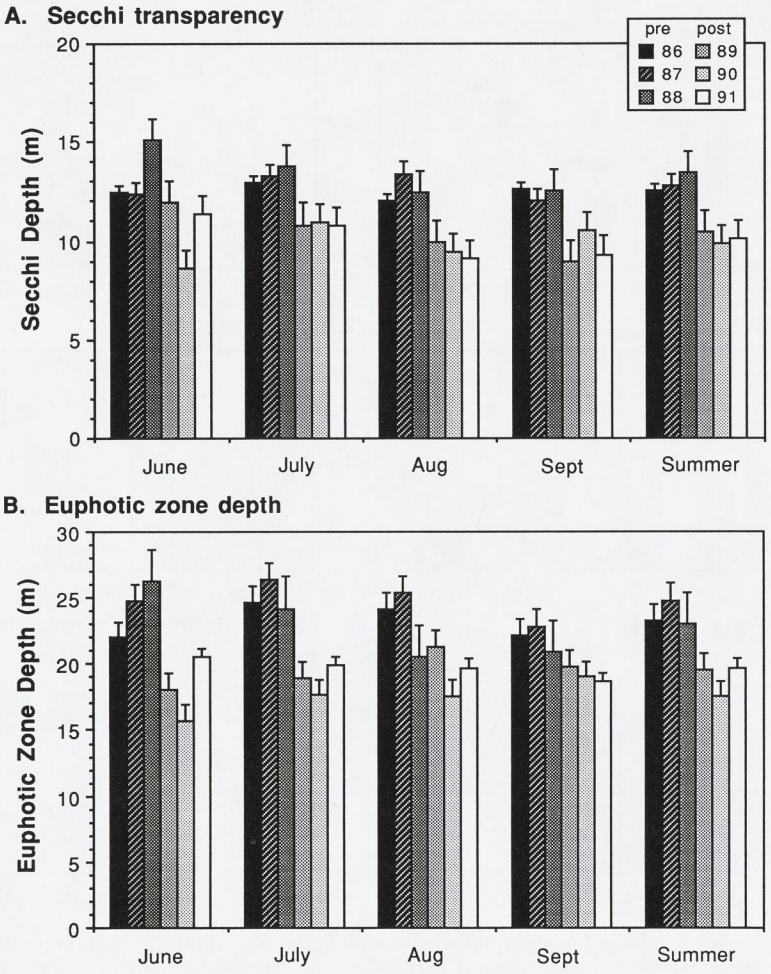

FIG. 8. As for Fig. 1, but for: (A) Secchi transparency, (B) depth of 1% light penetration (euphotic zone).

trout in Castle Lake does not detract from our inferences concerning the effect of this species on food web structure and function. Rainbow trout are representative of other species whose recruitment success is relatively constant (Cushing 1982) or species in which one strong cohort dominates the fish assemblage for many years (Carpenter et al. 1989, Rudstam et al. 1992). In these examples, the effect of the fish popu-

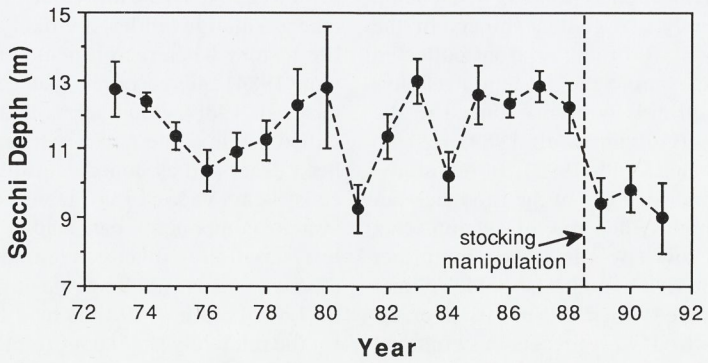

FIG. 9. Long-term dynamics of late summer Secchi transparency (mean for August–September observations) in Castle Lake, 1973–1991. Error bars indicate 95% confidence limits.

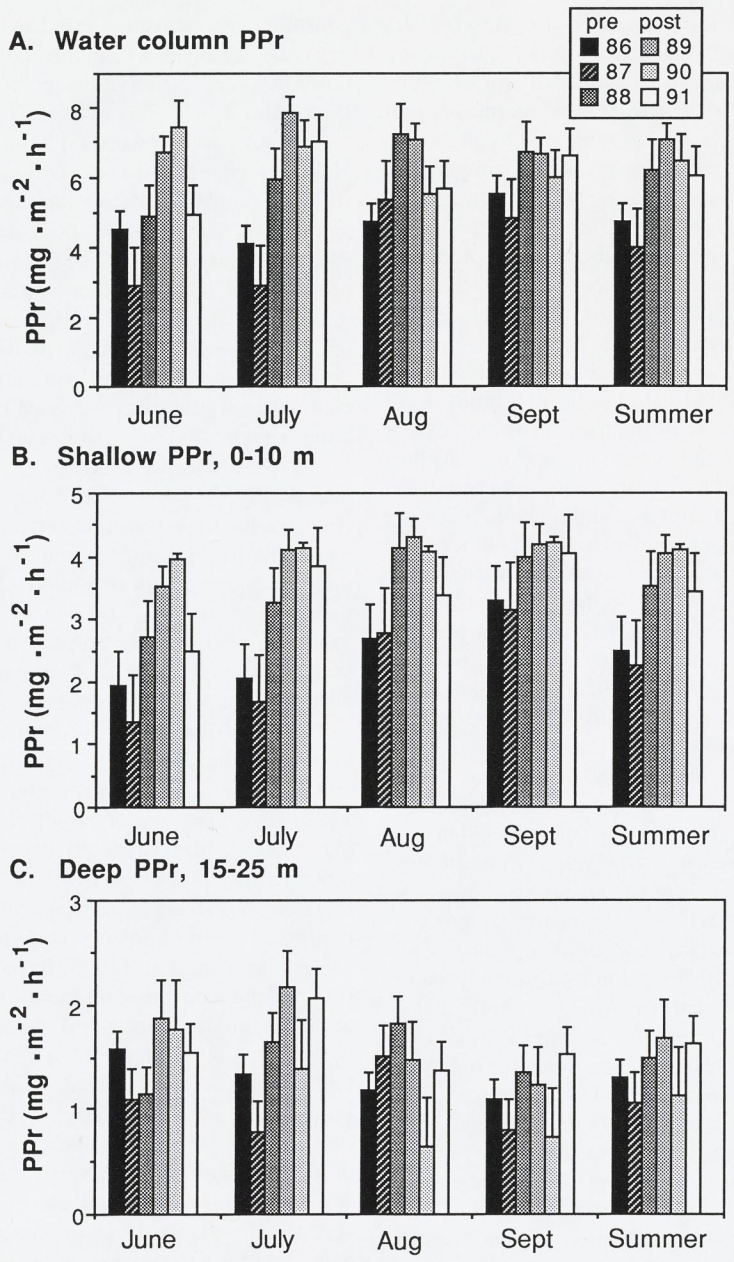

FIG. 10. As for Fig. 1, but for: (A) areal primary productivity (PPr, measured as carbon) for the entire water column, (B) areal PPr for the upper water layer (0–10 m), (C) areal PPr for the lower water layer (15–25 m).

lation is relatively constant as long as the species is present. We view the artificially maintained recruitment of rainbow trout in Castle Lake as an advantage in understanding species interactions. This relatively constant recruitment has allowed us to uncouple the dual role that climatic variation can play in food web function, that of adding variation to both fish recruitment and lake productivity (Carpenter et al. 1989). In years when rainbow trout are stocked at a constant rate, variation in lake productivity can be more easily attributed to climatic factors (Strub et al. 1985), whereas large changes in the stocking program can be followed through several years to assess top-down effects on ecosystem function (this study). Our results indicate that changes in stocking rate of rainbow trout affect a variety of ecosystem components in ways that cannot be explained by climatic variation.

A number of other instances of strong species interactions involve examples of predators that also share resources with their prey. Neill (1984) describes how

recruitment of the planktivorous insect *Chaoborus* depends on the competitive interaction of early-instar *Chaoborus* and *Daphnia* in lakes in British Columbia. Luecke et al. (1990*b*) describe how recruitment of bloater chub *Coregonus hoyi* is regulated by predation and competition with alewives in Lake Michigan. The large increases in abundances of golden shiner and brook trout after rainbow trout stocking was discontinued suggest that a similar combination of predatory and competitive effects of rainbow trout on other fish planktivores was important in determining the fish assemblage in Castle Lake.

The most dramatic and immediate response of the Castle Lake zooplankton to alterations in rainbow trout stocking was the increase in the previously rare cyclopoid *D. thomasi* (Fig. 2B), which are herbivorous during juvenile stages but predatory on various zooplankton taxa as late copepodids or adults (Pennak 1989). This increase, then, is potentially the result of increased food availability for juvenile stages due to increased brook trout and golden shiner predation on crustacean herbivores potentially in competition with juvenile *Diacyclops*. This possibility seems unlikely given the observed dynamics: *D. thomasi* increased dramatically in spring 1989 following the omission of the normal fall stocking in 1988 (Fig. 7A) but increased planktivory by brook trout and shiners was not observed until 1991 (Fig. 6) and *Daphnia* did not decline appreciably until late 1990 (Fig. 7C). An alternative explanation for the sudden appearance of *Diacyclops* in early 1989 is that, prior to the manipulation, large numbers of *Diacyclops* recruited from benthic resting stages (cyclopoids overwinter as late copepodids or adults; Pennak 1989) but predation by rainbow trout fingerlings normally kept pelagic densities of *D. thomasi* at low levels prior to the manipulation. While cyclopoid copepods would not be preferred prey items for fish when present in a mixed zooplankton assemblage, upon emergence adult and late-instar *D. thomasi* would be the first relatively large zooplankters available for trout fingerlings in early spring. While previous studies have shown that the abundance of cyclopoid copepods can increase strongly following reduction in planktivorous fish populations (Hansen and Jeppesen 1992, Lathrop and Carpenter 1992), the mechanism responsible for the rapid increase in *Diacyclops* following cessation of trout stocking to Castle Lake remains uncertain. We cannot directly test the spring predation hypothesis with our current data as we do not have diet samples for underyearling trout during premanipulation years. Trout stocking has recently been resumed at Castle Lake; further sampling may resolve this issue.

Changes in Castle Lake's water clarity and primary productivity following stocking manipulation illustrate further complexities in understanding how the functioning of pelagic ecosystems responds to alterations in food web structure. Just as reciprocal changes in the abundance of alternative predator taxa provide a compensatory mechanism within the food web itself, compensatory changes within the ecosystem render certain processes conservative in response to perturbation (Schindler 1987). The effects of the manipulation on water transparency were rapid and strong (Figs. 8–9). However, changes in water column primary productivity were somewhat more ambiguous (Fig. 10). The mechanism for the conservative nature of water column PPr in this case seems clear: the manipulation increased productivity in the surface waters (Fig. 10B) but reduced light penetration to light-limited deeper waters (Fig. 8B), lowering the contribution of deep water layers to total water column productivity (Fig. 10). Thus, changes in productivity integrated over the whole water column were modest, as increases in PPr in upper water layers were compensated for by decreases in PPr in deeper layers. As a result of these compensatory changes, the food-web-induced changes in productivity were small relative to the range of variation in summertime productivity documented by the nearly 30-yr data record analyzed by Jassby et al. (1990). More extensive analyses that correct for the contributions of serial autocorrelation and climate variation will be needed for a fuller assessment of the PPr response.

Previous considerations of the effects of CTI on ecosystem productivity have primarily focused on interannual variability (Carpenter et al. 1985, Carpenter 1988). However, the apparent effects of the stocking manipulation on the depth distribution and seasonal development of PPr in Castle Lake indicated that in this case the effects of manipulation were more strongly expressed on intra-annual rather than interannual time scales. Persson et al. (1993) have also emphasized the role of food web structure in modulating seasonal variation in aquatic ecosystems. In this sense the results we present here support the correlative evidence of Goldman et al. (1989) and Jassby et al. (1990) that climatic influences strongly govern interannual variation in ecosystem productivity but food web parameters produce variation in the vertical distribution and seasonal development of productivity in this system. More specifically, the analyses of Jassby et al. (1990) indicated that food web parameters predominantly affected productivity in the surface waters late in the stratified season. Numerous aspects of our observations support this correlative evidence: highest planktivory rates by young-of-the-year fishes in late summer months (Fig. 6), significant changes in *Daphnia* seasonality before and after the manipulation, strongest reductions in Secchi transparency in August/September (Fig. 8A), strongest PPr responses in the surface waters (Fig. 10), and significant changes in PPr seasonality before and after the manipulation. Thus, although alterations in patterns of phytoplankton productivity induced by our food web manipulations occurred through a different set of mechanisms than had been operating in Castle Lake during the time interval encompassed by the analyses of Jass-

by et al. (1990), it appears that the nature of the productivity response was largely the same.

The dynamics of fish and zooplankton populations, along with accompanying changes in water quality parameters, in Castle Lake following food web manipulation lead us to propose an alternative mechanism for cascading effects of top predators on phytoplankton productivity and water clarity. Previous considerations of CTI have emphasized the central role of *Daphnia* in affecting water quality (Carpenter et al. 1985, Lammens et al. 1990). Our observations indicate that *Daphnia,* or other large crustacean herbivores, need not be involved in altering water quality parameters when food webs are changed: decreases in water transparency were observed early in 1989 (Fig. 8) while *Daphnia* biomass did not decline appreciably until late 1990 (Fig. 7C). We hypothesize that effects on productivity and water clarity observed in 1989 resulted from the effects of increased *D. thomasi* predation on microconsumers (rotifers, ciliates, other protozoa), reducing microconsumer grazing pressure. Studies supporting this hypothesis include a series of enclosure experiments we have performed during 1991–1993 but are too extensive to include in this paper. We summarize the conclusions here. First, experimentally enhanced densities of *D. thomasi* produced strong declines in rotifer and ciliate densities in several experiments (Brett et al. 1994, Wiackowski et al. 1994). Second, measurements of micrograzer herbivory (grazing by consumers passing a 85-μm screen) made with dilution techniques (Landry and Hassett 1982) indicated microconsumer grazing rates of ≈0.10–0.25 d^{-1} (mean: 0.13 d^{-1}) on phytoplankton biomass (Elser and Frees 1995), greater than previous grazing rate estimates made for the crustacean herbivore assemblage in Castle Lake (0.06–0.12 d^{-1}, mean: 0.076 d^{-1}; Elser 1992). These microconsumer estimates were made in 1992, after the increase in *Diacyclops* abundance in Castle Lake; thus, microconsumer grazing pressure may have been even higher in years prior to manipulation. Finally, when plankton from a nearby lake without *Diacyclops* was exposed to *Diacyclops* for 10 d, the abundance of herbivorous ciliates and microherbivory rates decreased and chlorophyll concentration and algal growth capacity increased (J. J. Elser, *unpublished data*). The evidence just summarized comes from small enclosures (≤20 L) and short-term incubations (≤ 2 wk); whether these experiments yield valid insights into observed dynamics in Castle Lake is subject to question given the known potential for misleading indications when extrapolating from small-scale, short-term studies to whole-ecosystem, long-term dynamics (Frost et al. 1988). Future observations of *Diacyclops* abundance, microconsumer dynamics, and ecosystem processes as Castle Lake responds to the resumption of trout stocking will permit us to evaluate whether the hypothesized mechanism is sound. Further experimentation by others working in nutrient-poor lakes would also be useful in establishing the generality of the unconventional multitrophic-level mechanisms we have proposed.

The results we have presented here have led us to revise our view of the functioning of the Castle Lake food web and its impacts on variation in ecosystem productivity. The correlative evidence presented by Jassby et al. (1990), in which productivity variation correlated with relative trout abundance and *Daphnia* biomass during 25 yr of relatively constant stocking intensity, initially suggested to us a simple chain of coupled predatory interactions in which rainbow trout functioned primarily as a predator on *Daphnia.* Thus, our expectation was that reduction in rainbow trout abundance would lower productivity and increase water clarity as a result of increased *Daphnia* grazing. However, the opposite effects occurred when trout were reduced, accompanied by major changes in other, previously unrecognized or unappreciated, components of the food web: *Diacyclops,* golden shiners, and brook trout. Our new view of the Castle Lake food web incorporates the trophic complexity that these unexpected responses have identified. This includes the prevalence of mixed predation–competition interactions throughout this web, especially those involving rainbow trout and three alternative planktivores (*Diacyclops,* brook trout, golden shiners). Thus, following stocking manipulation of rainbow trout in Castle Lake, food web adjustments compensated for the reduction in the historically dominant planktivore to such a degree that the overall intensity of planktivory was higher following the manipulation, resulting in increased PPr and decreases in water clarity. The complex dynamics that we have documented here suggest that compensatory mechanisms involving rare or undocumented components of lake food webs (such as invertebrate predators and microconsumers, which are not considered in many studies) may be responsible for divergent or surprising outcomes when top predators are altered. Considerable debate has occurred regarding the impact of food web processes on phytoplankton dynamics as a function of lake trophic status (McQueen et al. 1986, Benndorf 1988, Elser and Goldman 1991, Carpenter and Kitchell 1993). Power (1992) has also noted that the relationship between ecosystem productivity and the potential influence of top-down forces is crucial in discerning among several competing theoretical frameworks describing food web interactions. Castle Lake may be the most oligotrophic lake yet subjected to a deliberate whole-lake food web manipulation. In low productivity lakes, low overall food availability at most links in the food web may enhance the potential for unexpected outcomes mediated by mixed predation–competition interactions.

Our results support the arguments made by Power (1992) and Strong (1992) that the trophic complexity of food webs in nature complicates predictions of the outcome of manipulations at the top of the food web:

reductions in densities of rainbow trout intended to reduce predation pressure on herbivorous zooplankton actually increased planktivore pressure (by both vertebrate and invertebrate planktivores). Nevertheless, alterations in the planktivory regime appeared to alter various water quality parameters. Our study also suggests alternative ways by which cascading effects can reach the bottom of the food web (i.e., microconsumer grazing altered by changes in the impacts of invertebrate predators) and emphasizes that food web effects on ecosystem processes are expressed at intra-annual as well as interannual time scales.

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Brett, M.T., C.R. Goldman, and S. Ayers. 1994. A limnological investigation of Whiskeytown Reservoir: potential impacts of temperature control curtains. Report to the US Bureau of Reclamation.

Brett, M.T., and C.R. Goldman. 1994. Crayfish population size and recolonization potential in the upper Sacramento River following the Cantara Vapam® spill, Report of 1993 field sampling. Report to the California Department of Fish and Game.

Brett, M.T., and C.R. Goldman. 1993. Crayfish population size and recolonization potential in the upper Sacramento River following the Cantara Vapam® spill. Report to the California Department of Fish and Game.

Brett, M.T., C.R. Goldman, and F.S. Lubnow. 1992. Effects of the Cantara Vapam® spill on the planktonic ecosystem of Shasta Lake. Report to the California Department of Fish and Game.

Scientific Writings for the General Public:

Brett, M.T. 1995. Castle Lake has record clarity. Mt. Shasta Herald. July 19, 1995. Newspaper article based on a press release I prepared.

Brett, M.T. 1994. Ongoing study keeps track of health of Castle Lake. The Dunsmuir News. page 2, Nov. 9, 1994. Newspaper article based on a press release I prepared.

Brett, M.T., et al. 1994. Cui-ui and ignorance. California Flyfisher July-August: 48-50. An article on the interests of conserving an endangered nongame fish versus a sport fishery.

Brett, M.T., et al. 1993 Welcome to Castle Lake. Interpretive brochure describing the natural history, aquatic ecology, and ongoing limnological research at Castle Lake, site of the University of California, Davis Limnological Research Station.

Successful Grant Proposals:

I have prepared a total of seven successful grant proposals. These include three proposals to the National Science Foundation (two at 90% and one at 40% effort), two proposals at 90% effort to the California Department of Fish and Game, and individual

proposals at 90% effort to the US Bureau of Reclamation and the private McConnell Foundation, and a final proposal (at 40% effort) to a local resource conservation district. The total amount of these proposals was over **$675,000**, with the majority coming from NSF. I also helped prepare (20% effort) a successful $40,00 proposal to the University of California Water Resources Center and I played a pivotal role in bringing a $300,000 contract from the US Bureau of Reclamation.

Invited Reviews:

I have been invited to review manuscripts submitted to several prominent journals including *Science, Nature, Limnology and Oceanography, Ecology, Canadian Journal of Fisheries and Aquatic Sciences, Transactions of the American Fisheries Society, Archiv für Hydrobiologie*, and *California Fish and Game*. I have also been asked to review several proposals submitted to the *National Science Foundation*.

Teaching Experience:

I taught the Principles of Environmental Science (EST 110) at the University of California, Davis. This is an upper division class with approximately 100 students. I independently developed the entire curriculum for this course on very short notice. The Department asked that I teach the principles of environmental sciences using current topical issues as examples. Because I am focusing on topical issues I was unable to find a textbook which fit the needs of the course. I therefore developed an extensive set of reading materials based exclusively on current primary and secondary literature. The topics covered have included the Philosophy of Science (Plato, Popper, Platt), The Tragedy of the Commons, The Collapse of Georges Bank, The Decline of Pacific Salmon, Coral Bleaching, The Endangered Species Act, Evolutionary Significant Units, The Spotted Owl Issue, Wetlands Delineation, Eutrophication, Desertification, Global Climate Change, Acidification, and Pending Land Reform Legislation. I have attempted to emphasize critical and independent thinking, as well as develop research and writing skills. I have found teaching this course to be one of the most challenging and rewarding endeavors I have undertaken during my entire career in academia.

While working towards my Ph.D. in Sweden, I taught the equivalent of several semesters of Scientific Writing. In graduate school and particularly while a PostDoc at UCD, I have given extensive guest lectures to Limnology courses. I also TA'd Introduction to Biology and Fisheries Biology courses at the University of Maine. I have also been very active in helping a local public school district incorporate environmental sciences into its science and mathematics curricula. This has included leading a teacher training seminar, hosting eight field trips, offering seminars to several High School classes, and developing an extensive interpretive display and brochure. During review of a recently funded NSF proposal the panel commented on "the excellent efforts at community outreach" which primarily relates to work I did as the supervisor of the Castle Lake Project. I have also worked as a research advisor to several undergraduate and graduate students, with several of these joint efforts resulting in publications.

Recent Responsibilities:

During my postdoctoral fellowship, I have been the supervisor of the Castle Lake Field Research Station and associated National Science Foundation grants. During the time I have managed the project, it has had approximately $150,000 yearly support from the National Science Foundation, with five to ten graduate students and undergraduate assistants in residence at the field station each summer. During this time, I also designed and supervised a limnological investigation of a pesticide spill's impact on a large reservoir, an investigation of the same spill's impact on the crayfish population of a river, as well an investigation of temperature-control curtain impacts on the limnology of a reservoir. I am currently analyzing a 20 year cutthroat trout growth and survival data set for Pyramid Lake, Nevada. I am also helping the Pyramid Lake Paiute Indian Tribe develop a comprehensive food web investigation to compliment their current trout growth rate and lake water quality investigations.

References:

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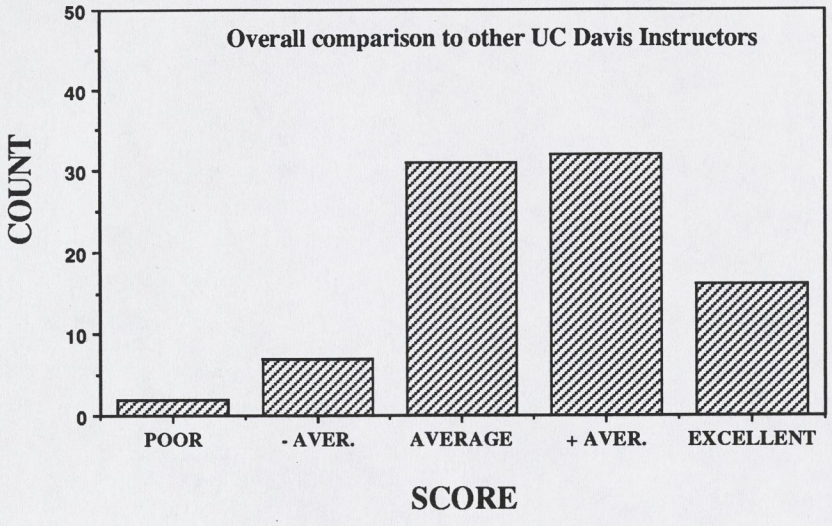
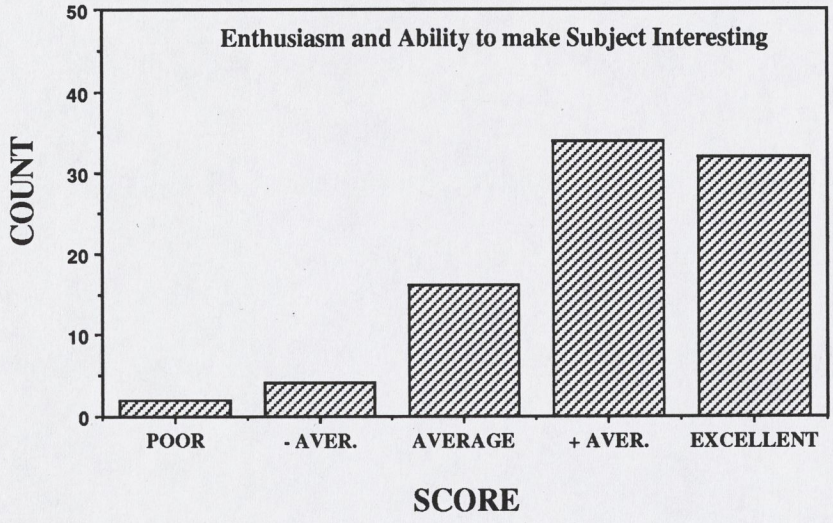
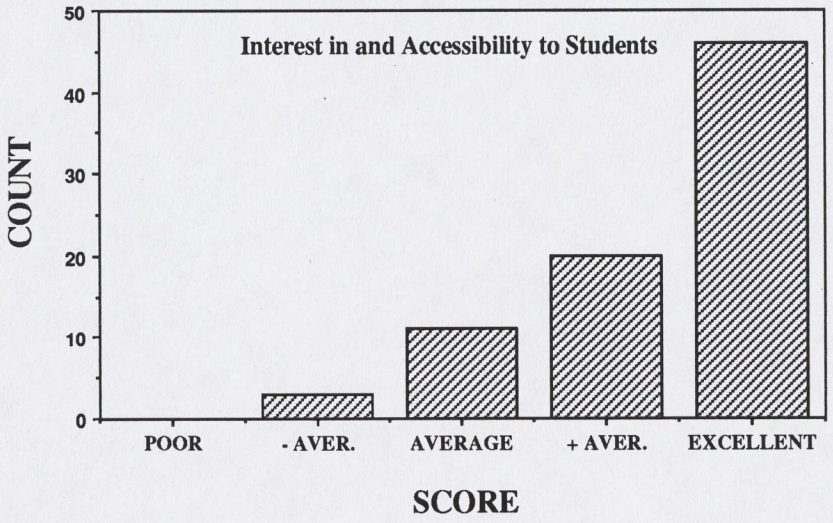
Michael T. Brett, 1995 Teaching Evaluations







[ca 1996]

A Quantitative Test of the Freshwater Trophic Cascade

Submitted to:
Proceedings of the National Academy of Sciences

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THE generality of the trophic cascade[1] has been an intensely debated topic amongst ecologists[2-4]. We conducted a meta-analysis of 41 separate enclosure experiments which measured the response of the zooplankton and phytoplankton to zooplanktivorous fish treatments. These results provide unequivocal support for the trophic cascade hypothesis in freshwater food-webs. Zooplanktivorous fish treatments resulted in reduced zooplankton biomass and increased phytoplankton biomass. The trophic cascade was not obviously dampened at the level of the phytoplankton. However, the phytoplankton's response to the trophic cascade was highly skewed with very strong responses in about half the cases and weak responses in the other cases.

Trophic cascade theory holds that each trophic level of a food-web is inversely and directly related to trophic levels above and below it[1]. For example, if the abundance of large piscivorous fish is increased in a lake, the abundance of their prey zooplanktivorous fish should decrease, large herbivorous zooplankton abundance should increase, and phytoplankton biomass should decrease. This theory has stimulated new research in many areas of ecology[4]. Trophic cascade theory was generated from empirical observations that piscivorous fish can dramatically reduce populations of zooplanktivorous fish, zooplanktivorous fish can dramatically alter freshwater zooplankton communities, and zooplankton grazing can in turn have large impacts on phytoplankton communities[5-8]. Almost from its first presentation this theory has been embroiled in a controversy over whether "top-down" (i.e. consumer) or "bottom-up" (i.e. nutrient) forces determine the structure of aquatic food-webs[4,9]. Based on the observation that many studies do not show statistically significant impacts of piscivorous or zooplanktivorous fish on the structure of freshwater food-webs, a recent critique

of this theory argued that "even the briefest perusal of the pertinent literature indicates that, far from being robust, the trophic-cascade theory may be unsoundly based on many half-truths and much hand-waving and overextrapolation of the data"[2].

DeMelo et al.'s critique[2] of trophic cascade theory used a technique for summarizing information from the literature called vote-counting. Vote-counting consists of simply tallying all studies which detect statistically significant effects and non-significant effects, and inferring the generality of a phenomena[10,11,12]. Although this technique is the most universal method of summarizing information from large bodies of literature in the ecological sciences, it has a fatal flaw in that is perpetuates all Type II statistical errors (or failing to detect a true effect) in the original studies. Because ecological field studies usually use small sample sizes and have high variability they are particularly susceptible to Type II errors[13,14]. We have analyzed the data from most of the studies cited by DeMelo et al., as well as many other studies, using a statistical technique called meta-analysis. Meta-analysis is a simple and robust approach to detecting central tendencies in large multi-investigation data sets[10,11,12]. By quantitatively summarizing and statistically testing information from many studies, this technique greatly reduces propagation of Type II errors.

In a search of the literature, we located 27 published studies which reported 41 separate enclosure experiments examining zooplanktivorous fish impacts on zooplankton and phytoplankton communities (see Appendix 1). We have restricted our analysis to enclosure and experimental pond studies because relatively few whole-lake investigations have been reported in the literature[2] and meta-analysis is most powerful when a large number of studies are compared[10,11]. Furthermore, long-term monitoring has shown that tremendous

variability in mean annual primary production in lakes can be due to serial autocorrelation, climatic impacts, and eutrophication[15-17]. This external variability is likely to obscure detection of a trophic cascade if only a small number of studies are compared.

Of the 41 published investigations of zooplanktivorous fish impacts on zooplankton and phytoplankton communities, 15 were not replicated, 20 were replicated but only reported treatment means, and 6 were replicated and reported treatment means, variability and sample size. Due to the nature of the available data we conducted two data analyses. The first was an analysis of the mean responses to fish treatments across all 41 separate experiments (Fig. 1). The second was a full meta-analysis according to Gurevitch and Hedges[11] utilizing treatment responses, variability and sample size information for the 6 fully replicated and reported investigations (Table 1).

The results of the data analysis employing all 41 enclosure experiments (Fig. 1) showed that in general the zooplanktivorous fish treatments resulted in greatly decreased zooplankton biomass; median = 25% of the control value. Similarly, the fish treatments resulted in increased phytoplankton biomass; median = 184% of control value. These results were strongly supported by a full meta-analysis of the 6 fully replicated and adequately reported experiments which showed the fish treatments reduced zooplankton biomass by 2.4 standard deviations and increased phytoplankton biomass by 2.9 standard deviations (Table 1).

The results of these analyses (Figs. 1 and Table 1) provide unequivocal support for the trophic cascade hypothesis in freshwater planktonic ecosystems[1]. These results should end the debate[2-4] over whether the trophic cascade is a general feature of freshwater food-webs and focus the attention of researchers on new questions, such as

explaining variation in the phytoplankton's response to the cascade. All of the studies summarized by us showed zooplankton biomass was depressed by zooplanktivorous fish treatments, while in 39 of 41 cases these same treatments increased the biomass of the phytoplankton. However, in many cases these effects were small, particularly for the phytoplankton, and would not be statistically detected by a study with no or few replicates and high variability. The lack of treatment effects noted by DeMelo et al.[2] appears to be mainly the result of low statistical power.

It should be noted, however, that enclosure experiments are not completely representative of lakes. Few studies employ enclosures which are open to the sediments and some planktivorous fish, in particular many Eurasian cyprinids, are known to actively stir up sediments. In addition, many of the analyzed experiments acknowledged that they used treatment fish abundances which were greater than those typically seen in the relevant lakes.

The present results do not support McQueen's contention[18] that the trophic cascade is strongly dampened at the level of the phytoplankton. Our statistical analysis (Fig. 1) indicates that any overall dampening in the phytoplankton's response to the cascade is quite small compared to the variability in the phytoplankton's response to the cascade, e.g. the dampening effect size was only 0.22 standard deviations or the phytoplankton response averaged 80% of the magnitude of the zooplankton response. This interpretation is also supported by the full meta-analysis (Table 1) which actually showed a slightly larger phytoplankton response.

The phytoplankton's response to the zooplanktivorous fish treatments was highly skewed (Fig. 2). The median phytoplankton response was an 84% increase in biomass while the geometric mean response was a 202% increase in biomass. The 20 cases where the phytoplankton showed the smallest response to the trophic cascade averaged only a 31% increase

in phytoplankton biomass, while the 20 highest responses averaged a 615% increase in phytoplankton biomass. In short, in about half the cases the impact of the trophic cascade on the phytoplankton was rather weak, while in the other half of the cases the impact on the phytoplankton was very strong.

Although we observed a wide range in the zooplankton's response to the cascade, variability in the phytoplankton's response was only very weakly inversely associated with variability in the zooplankton's response (linear regression: $R^2 = 0.052$, F-test = 2.12, n = 41, P = 0.15). This result is not consistent most interpretations of trophic cascade theory. In some cases small decreases in zooplankton biomass corresponded to large increases in phytoplankton biomass, while in other cases large decreases in the zooplankton corresponded to small increases in the phytoplankton. Dominance by large zooplankters like *Daphnia* may increase the zooplankton's impact on the phytoplankton, and dominance by colonial cyanobacteria may minimize the phytoplankton's susceptibility to grazing by zooplankton. Unfortunately, most of the experiments reported in the present study did not present the composition of the zooplankton and phytoplankton communities in sufficient detail to make a comprehensive quantitative assessment of the role of the zooplankton and phytoplankton composition in determining the strength of the trophic cascade.

Although our results strongly support trophic cascade theory, they provide weaker support for the idea that manipulations of fish communities can be used to consistently control algal biomass in lakes (e.g. biomanipulation). <u>The new challenge to aquatic food-web researchers is understanding why the response of the phytoplankton to the trophic cascade is so variable.</u>

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TABLE 1 Results for full meta-analysis for six enclosure experiments

Publication	Fish species	Source	Parameter	Effect Size d	Variance v	Weight w	w^2	wd	wd^2	v*	w*	w*d
Zooplankton												
Castle Lake, unpubl.	golden shiners		Crustacean Bm.	-3.88	1.92	0.52	0.27	-2.02	7.83	2.12	0.47	-1.83
Christoffersen 1993	roach	Fig. 8	Crustacean Bm.	-3.00	2.13	0.47	0.22	-1.41	4.24	2.33	0.43	-1.29
Vanni and Findlay 1990	yellow perch	Table 2	Crustacean Bm.	-6.60	4.30	0.23	0.05	-1.54	10.14	4.50	0.22	-1.47
Leibold 1989	bluegill	Fig. 5	Daphnia abund.	-3.71	2.72	0.37	0.14	-1.36	5.06	2.92	0.34	-1.27
Lynch 1979	bluegill	Fig. 3	Crustacean Bm.*	-0.64	0.56	1.79	3.20	-1.14	0.73	0.76	1.31	-0.84
Hurlbert et al. 1972	mosquitofish	Table 1	Crustacean Bm.*	-2.37	1.14	0.88	0.77	-2.09	4.96	1.34	0.75	-1.77
Phytoplankton												
Castle Lake, unpubl.	golden shiners		Chl a	1.45	0.84	1.19	1.41	1.72	2.50	0.99	1.01	1.46
Christoffersen 1993	roach	Fig. 8	Biovolume	3.04	2.16	0.46	0.21	1.41	4.29	2.31	0.43	1.32
Vanni and Findlay 1990	yellow perch	Table 3	Biovolume	5.67	3.35	0.30	0.09	1.69	9.61	3.50	0.29	1.62
Leibold 1989	bluegill	Fig. 3	Chl a	2.55	1.82	0.55	0.30	1.41	3.59	1.97	0.51	1.30
Lynch 1979	bluegill	Fig. 5	Biovolume	2.97	1.09	0.92	0.85	2.74	8.14	1.24	0.81	2.41
Hurlbert et al. 1972	mosquitofish	Table 1	Coccochloris	10.61	10.06	0.10	0.01	1.06	11.20	10.21	0.10	1.04

Summation of mixed model results

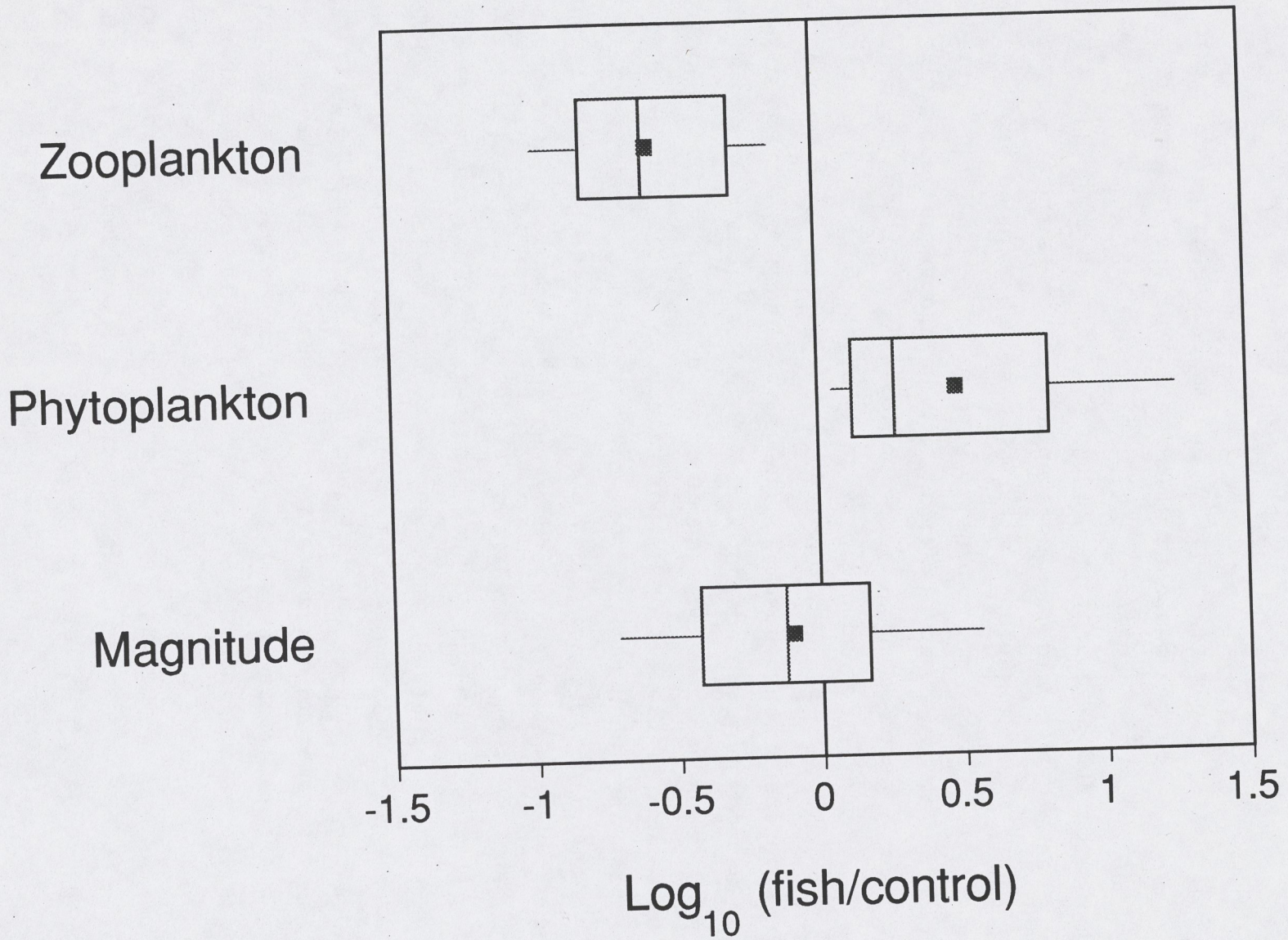
	Effect Size d+*	Variability SD(d+*)	99% C.I. ±	Heterogeneity Q
Zooplankton	-2.40	0.53	1.25	11.50
Phytoplankton	2.91	0.56	1.37	10.78

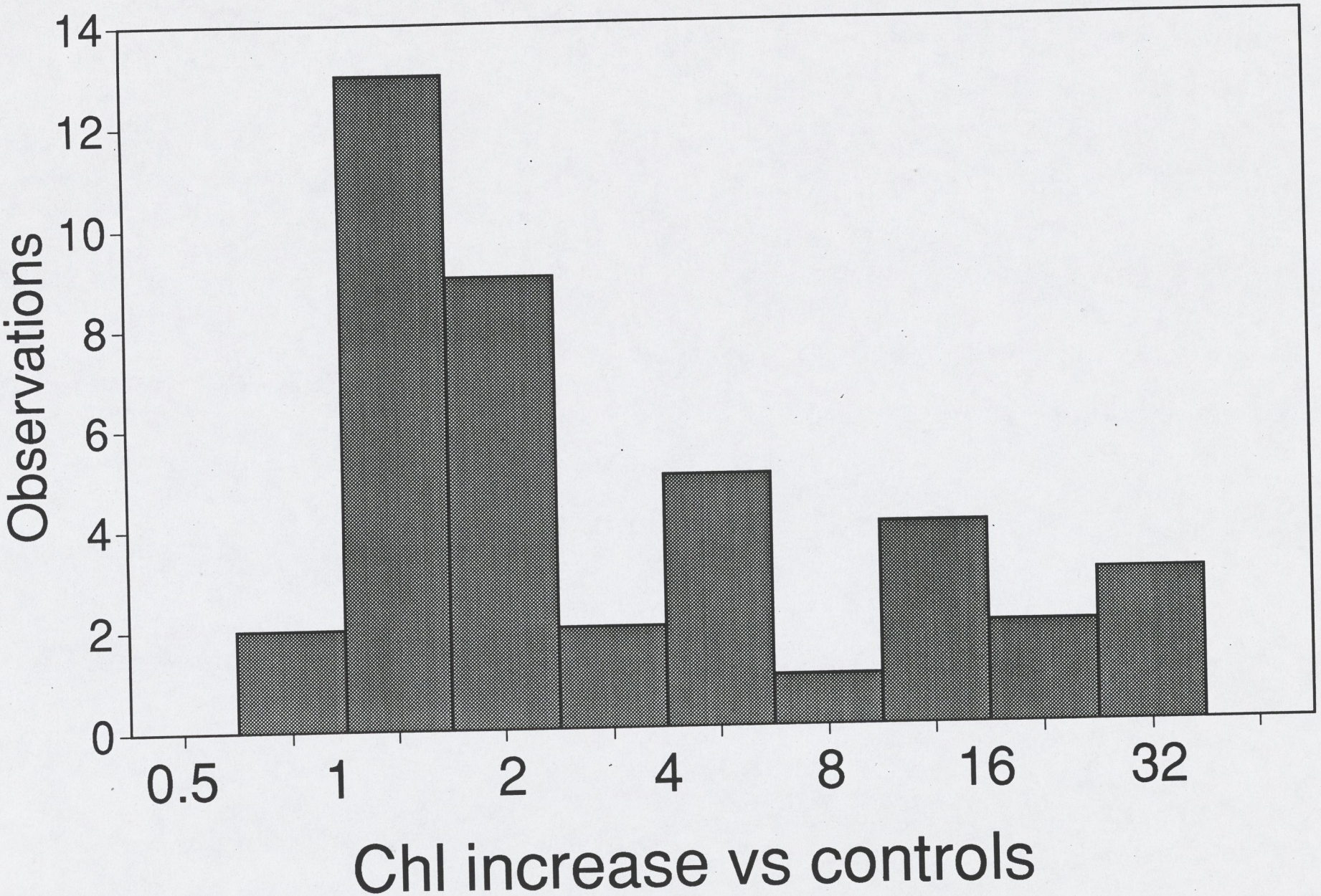
*Biomass estimated by assuming weights for specific taxa.

Results of a full meta-analysis of the 6 fully replicated and reported enclosure experiments according to Gurevitch and Hedges[11]. This analysis showed the average decrease in zooplankton biomass in the zooplanktivorous fish treatments was -2.40 standard deviations, while the average increase in phytoplankton biomass was 2.91 standard deviations. The results for both the zoo- and phytoplankton were highly statistically significant, i.e. the 99% confidence intervals did not come remotely close to overlapping zero. The test of homogeneity (Q statistic which approximates a χ^2 distribution) between experiments was moderately significant for both the zooplankton ($P < 0.05$) and phytoplankton ($P < 0.1$) responses. This suggests that there is not a fixed average effect about which all results randomly vary, but instead suggests that there is a general response and real differences between experiments which are not solely due to random processes.

FIG. 1 Averaged responses of the zooplankton and phytoplankton to zooplanktivorous fish treatments for all 41 enclosure experiments. The line through the middle of the box shows the median and the dot shows the mean of the distribution. The outer edges of the box correspond to the 25th and 75th percentiles, and the "whiskers" to the 10th and 90th percentiles. Only studies which utilized concurrent zero fish controls were used. When multiple fish treatment levels were used, we compared the high fish to the control treatments. We did not use data from any treatments where the authors reported significant mortality of treatment fish or where nutrients were added. The data from each experiment were "scaled" by dividing the mean values from the fish treatment by the corresponding control values. Total crustacean zooplankton biomass was used to characterize the response of the zooplankton; however, when this parameter was not presented we used total zooplankton biomass, large crustacean biomass, or large zooplankton abundance, etc. Similarly, chlorophyll concentration was preferentially used to characterize the phytoplankton response; however, in some cases phytoplankton biovolume, primary production, or fluorescence was used instead. Magnitude, a measure of whether the cascade is dampened or heightened at the phytoplankton level, was calculated by adding the $\log_{10}$ transformed phytoplankton response to the $\log_{10}$ transformed zooplankton response. The data were tested against a null hypothesis of no effect by comparing $\log_{10}$ transformed data (fish/control) against a hypothetical population mean = 0. The zooplanktivorous fish treatments resulted in greatly decreased zooplankton biomass (t-value = -11.05, n = 41, $P < 0.0001$), and increased phytoplankton biomass (Wilcoxon sign-rank test, $z = 5.37$, n = 41, $P < 0.0001$). The magnitude of the phytoplankton's response was not significantly different from the hypothetical mean of zero (t-value = -1.43, n = 41, $P = 0.16$).

FIG. 2. The frequency distribution of the phytoplankton's response to the planktivorous fish treatments.


Zooplankton
Phytoplankton
Magnitude
-1.5
-1
-0.5
0
0.5
1
1.5
Log10 (fish/control)


Observations
14
12
10
8
6
4
2
0
0.5
1
2
4
8
16
32
Chl increase vs controls

APPENDIX 1:

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TABLE 1 Results for full meta-analysis for six enclosure experiments

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Hurlbert et al. 1972	mosquitofish	Table 1	Crustacean Bm.*	-2.37	1.14	0.88	0.77	-2.09	4.96	1.34	0.75	-1.77
Phytoplankton												
Castle Lake, unpubl.	golden shiners		Chl a	1.45	0.84	1.19	1.41	1.72	2.50	0.99	1.01	1.46
Christoffersen 1993	roach	Fig. 8	Biovolume	3.04	2.16	0.46	0.21	1.41	4.29	2.31	0.43	1.32
Vanni and Findlay 1990	yellow perch	Table 3	Biovolume	5.67	3.35	0.30	0.09	1.69	9.61	3.50	0.29	1.62
Leibold 1989	bluegill	Fig. 3	Chl a	2.55	1.82	0.55	0.30	1.41	3.59	1.97	0.51	1.30
Lynch 1979	bluegill	Fig. 5	Biovolume	2.97	1.09	0.92	0.85	2.74	8.14	1.24	0.81	2.41
Hurlbert et al. 1972	mosquitofish	Table 1	Coccochloris	10.61	10.06	0.10	0.01	1.06	11.20	10.21	0.10	1.04

Summation of mixed model results

	Effect Size d+*	Variability SD(d+*)	99% C.I. ±	Heterogeneity Q
Zooplankton	-2.40	0.53	1.25	11.50
Phytoplankton	2.91	0.56	1.37	10.78

*Biomass estimated by assuming weights for specific taxa.

Results of a full meta-analysis of the 6 fully replicated and reported enclosure experiments according to Gurevitch and Hedges[11]. This analysis showed the average decrease in zooplankton biomass in the zooplanktivorous fish treatments was -2.40 standard deviations, while the average increase in phytoplankton biomass was 2.91 standard deviations. The results for both the zoo- and phytoplankton were highly statistically significant, i.e. the 99% confidence intervals did not come remotely close to overlapping zero. The test of homogeneity (Q statistic which approximates a χ^2 distribution) between experiments was moderately significant for both the zooplankton ($P < 0.05$) and phytoplankton ($P < 0.1$) responses. This suggests that there is not a fixed average effect about which all results randomly vary, but instead suggests that there is a general response and real differences between experiments which are not solely due to random processes.

Ed Henke
Historical Research
769 Lisa Lane • Ashland, Oregon 97520 • 541-482-9578

March 2, 1998

Dr. Robert J. Behnke
Department of Fishery and Wildlife Biology
Colorado State University
Fort Collins CO 80523-1474

Dear Dr. Behnke

Thanks so much for your generous amount of attention and comments of January 28 regarding my various pieces of correspondence to you. It certainly reinforces my interest in the "Historical Research" project as a neophyte and somewhat of an interloper in your wonderful profession.

I have been very determined about acquiring as much documentation as I can relative to these various "runs/groups" of anadromous salmonids entering the Southern California coastal creeks and rivers. My own personal experiences, combined with the documentation obtained to date, continue to create a lot of motivation in this regard. Your explanation of the Klamath half-pounders and their life cycles is congruent with Southern California, except in such a semi-arid region, resulting from the geological changes combined with the dewatering of almost all of the rivers, no evidence remains to substantiate such a life cycle except by capturing it through anecdotal and oral history means.

I can sure see why you're a professor. You know Erhard Rostlund and Lord Kelvin, and their professional limitations. Yes, my calculations were assumed to totally fit into your "by chance" category, but knowing firsthand and through my numerous (70) "oral history" sessions, the populations densities had to be many times the estimates made by a very few fairly contemporary professionals. You are so right in your judgment that one of my prime purposes in this "research" was to combine and dramatize the social significance of the Southern Steelhead and the specific habitat (creeks/rivers) they occupied which would lead to fortifying my historical population density estimates of this species (and others). You were very gentle and encouraging in your last statement that fishery biologists would not find fault with this effort.

The article "Why Aren't There More Atlantic Salmon?" was very applicable to my efforts. Missing pages 7-8 on this one. Also, "Egg-To-Smolt Survival and Fry-to-Smolt Density Dependence of Keogh River Steelhead Trout" very enlightening. Thank you for all.

Enclosed is another personal effort to get at the core problem of natural resource management in California. If you haven't already met Jack Fraser, I would encourage you to have a visit. He's a very special person, and you two would really complement each other.

Again, many thanks for your educational assistance and personal evaluations of my passion for this special life form.

Best to you.

Sincerely,

Ed Henke

Ed Henke
Historical Research
769 Lisa Lane • Ashland, Oregon 97520 • 541-482-9578

March 2, 1998

As a very concerned citizen regarding the potential extirpation of much of California's native flora and fauna, I have long since left the confines of healthy skepticism, finding myself bound up by solicitude and harboring an unhealthy cynicism. However, this negative stuff has served to create a good level of motivation and optimism from within. The enclosed presentation by Jack Fraser left me energized and motivated to share it with people like you who would possibly be inclined to push Jack's thoughts with some vigor and into the political arena for change… Jack has given me his blessing to circulate this presentation as I see fit.

As Jack has advocated, we need less politics and more good science to guide the management of our natural resources, "**PUBLIC TRUST ASSETS.**" As an advocate of wise and prudent use of such resources, he has shared with us a composite of thoughts that are a masterpiece of organization, profound in reasoning, unworthy of any challenges as to the accuracy of its substance, and containing a rationale that can stand tall in the face of all criticism. I told Jack that he had created an "Emancipation Proclamation" for fish and wildlife resources.

Time has almost run out for much of California's native flora and fauna/fish and wildlife resources. We need some positive action now, with immediate efforts more on offensive restoration than continuing to fight a losing defensive effort against destruction. Reorganizing and reconstituting how California manages its natural resources as advocated by Jack Fraser would be a best first step toward accomplishing this, as well as the best long-term solution.

Thank you for responding to Jack's unselfish efforts. He has given us a strong moral compass to follow and the organization to keep it on course.

Best personal regards.

Sincerely,

Ed Henke

Tongues Retell the Story Of New World Migration

By Richard Cole
Associated Press

Berkeley

A decade ago the history of the first humans to reach the New World seemed to be set in anthropological stone.

Scientific doctrine held — and U.S. children were taught — that the ancestors of Native Americans crossed the Bering Strait from Asia 11,000 or 12,000 years ago, after the last ice age, then fanned out across two continents.

But in 1989, University of California at Berkeley linguist Johanna Nichols began the first systematic look at Indian tongues.

Prehistory was very wrong, she quickly decided.

She found 150 language families in North and South America — half the world's total. And languages take time to develop and split into new tongues.

"I knew perfectly well that there's no way you could get 150 such language families in here, of such different types, in that time," Nichols says. "Whatever the age of the languages is, it's a great deal more than 11,000 years."

In fact, her studies suggested the Americas had actually been inhabited for 30,000 or 40,000 years, and there were sever-

LANGUAGE: *Page A17 Col. 1*

San Francisco Chronicle
WEDNESDAY, MARCH 18, 1998

From Page A15

al separate migratory waves.

Nichols joined a small chorus of scientists who challenged orthodox anthropology and archaeology, and who were initially dismissed by the mainstream.

But within years, microbiologists tracking DNA in Indian tribes announced similar conclusions. And the discovery of a 12,500-year-old settlement in Monte Verde, Chile — a location which would have taken at least 6,000 years for Asian settlers to reach — set back the date of the New World's human habitation by thousands of years.

At an American Association for the Advancement of Science conference last month, Nichols and other scientists on a panel discussing the first Americans found their once-rejected theories are now the mainstream.

David Meltzer, a Southern Methodist University archaeologist and early believer in older migrations, praises Nichols' work.

"It's converging with archaeological evidence to the point that we're starting to feel reasonably confident that we have humans in the New World prior to 20,000 years ago," he says.

Nichols, a soft-spoken Iowa native who began her career teaching Slavic languages at Berkeley in 1972, doesn't gloat about her victory. She'd rather explain her theories.

Tracing language families — sometimes based on something as arcane as how numbers were used, where a verb is placed in a sentence, or the "m" sound in pronouns — can give insights into migration patterns, she says.

Like the patterns she helped establish, Nichols' interest in the New World started in Asia. As a Slavic language expert, she was in Asia in 1989 looking at languages in the Caucasus mountains. She decided to research how Asian languages evolved in the Americas.

At the same time, she was exploring a mathematical pattern in how languages evolved into new tongues.

"On average, every 6,000 years, each of the oldest language families split into 1.5," she says. By dividing the number of language families by that factor, she could come up with a good estimate of how far back an area was settled.

"It's almost idiotically simple, but no one had ever done it before," Nichols says.

A pattern emerged from Native American languages. The first wave or two of migrants from Asia arrived 30,000-40,000 years ago, before the last ice age, which lasted from 22,000 to 14,000 years ago.

They spread out — although perhaps thinly — through the Americas. When the ice sheets spread south thousands of years later, the first Americans apparently huddled in South America to wait out the climate change.

After the ice age, those migrants spread north again. Although there is insufficient evidence to establish a trail, Nichols can trace the origin of the Great Plains Indian tribes, such as the Sioux.

Their languages seem descended from the Southwest tribes such as the Apache and Navajo.

"After the end of glaciation, it looks to me like language spread north from somewhere — perhaps the Gulf Coast or Central America — into North America," she says.

As the first settlers headed north, a new wave of immigrants was arriving across the Bering Strait from Asia. They were different both in language and culture from the older natives, and seemed to stick to the coastline.

"In the New World, there's a narrow strip running down the entire length of the western coast, more or less, with language features imported relatively recently from Asia," says Nichols. Recently meaning 11,000 to 12,000 years ago.

Those newer immigrants apparently didn't mix east of the Sierra Nevada in North America and the Andes in South America, her studies showed.

In a final migration wave, the ancestors of modern-day Eskimos arrived from Asia about 5,000 years ago. Perhaps because the area to the south was now inhabited, they stayed to the north in what is now Alaska, Canada and Greenland.

Around the world, archaeological finds seem to show that modern human migration, which apparently started in Africa 100,000 to 120,000 years ago, occurred much faster than once believed. Sites in Australia have now been pushed back to 50,000 years ago, Nichols says.

Her studies also show one other intriguing result. By using the same calculations that established New World migration dates, she estimates that the world's languages could have developed over a 120,000 year period.

Does that mean there is an ancient mother tongue?

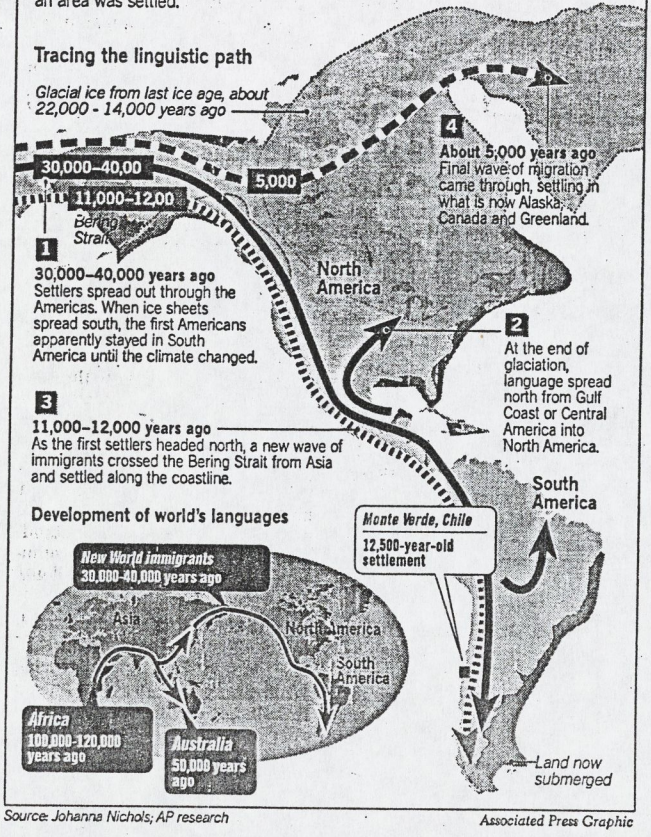
Nichols is cautious.

"It could be that all the world's languages accidentally go back to just one of the ones that was spoken then," she says. With the tools available to linguists today, she emphasizes, there is no way to be certain.

But if anyone ever develops the necessary tools, it is likely to be Johanna Nichols.

LANGUAGE ANCESTORS OF THE AMERICAS

Linguist Johanna Nichols used a mathematical pattern to determine how Asian languages evolved in the New World. She concluded that the ancestors of Native Americans crossed the Bering Strait into the New World 30,000 to 40,000 years ago.



Source: Johanna Nichols; AP research

Associated Press Graphic

THE GOVERNANCE OF WILDLIFE RESOURCES AND "UNCROOKING" THE SYSTEM[1]

By

Jack C. Fraser[2]

My name is Jack C. Fraser. I reside in Fountain Hills, Arizona. I am not representing any organization but I am very concerned about the future of our wildlife resources. I formerly served the California Department of Fish and Game in positions ranging from biologist to Regional Manager and Branch Chief. I retired in 1976. I have also served as Chairman of the Environment Protection Authority of the State of Victoria, Australia and as an international environmental consultant in ten foreign countries, the United Nations and in the U.S.

First, let me commend the Commission for engaging in this introspective planning effort. I also compliment you on seeking public input. Your examination of Commission responsibilities will undoubtedly lead to some improvements but I cannot help but ask whether a strategic planning approach, by itself, can overcome a fundamental weakness in the California system of wildlife resource governance. I submit the answer to that question is no! I trust you will be patient with my frank and sometimes blunt explanation.

Wildlife Resources in Rapid Decline

Over the many years I have been involved in wildlife and environmental management, I have observed a tragic evolution and appalling decay in wildlife resource governance, not only in California but throughout the western states. Recognition of fish and wildlife as a public resource of importance to all people and keeping the decision-making process in the public arena have been replaced by "politically correct" governance carried on behind closed doors, and related more to the political agenda of the day than to the health of the resource. Advocacy for protection of the resource from within government has declined. An atmosphere of substituting public relation exercises and artificial means of maintaining the resource, or even selling or trading the resource to gain a political edge for some other objective of the moment, has become commonplace. The public is seldom aware of these happenings because many occur without or with minimal exposure or they can be subtle changes over time (e.g. the 1995 Strategic Plan of the Department is a classical example of wildlife management driven by a public relations approach. Mitigation banking and many mitigation decisions can be cited as public resource giveaways.)

Presented

[1] ~~Prepared for presentation~~ to the California Fish and Game Commission, Sacramento, California, January 16, 1998

[2] Address: 14956 E. Windyhill Road, Fountain Hills, Arizona 85268 Tel: (602) 837-3026 Fax: (602) 837-6305.

Attempting to placate a declining constituency of consumptive users has caused fish and wildlife agencies to increasingly engage in public relations exercises and actions contributing little or nothing to the resource they are charged with protecting but diverting attention and funds away from solving fundamental resource problems. It has been a steady progression of irresponsibility for the resource by the agencies charged with the trusteeship. This irresponsibility has been a major contributor to the appalling downward spiral in fish and wildlife resources.

The California Situation

A significant acceleration in this trend took place after the California Department of Fish and Game was placed under the Resources Agency. Major resource policy decision-making was gradually taken away from the Commission and increasingly made in the political chambers and not in the public forum of Commission meetings. Gradually the Commission has been relegated to a comparatively unimportant role in relation to formulating and enforcing resource protection policy. The Director is answerable, not to the Commission, but to the political agenda of the day.

Thus there has been a deterioration from decisions made in public forum, with public input and understanding, to closed-door policy formulation. All too often the resource becomes the sacrificial lamb without public knowledge. Professionalism in the Department has declined along with a sense of responsibility for the basic resource. Professionalism in the hierarchy of the Department has been progressively displaced by a political hackdom increasingly unresponsive to public desires for resource trusteeship and incapable of providing advice other than that which has received political filtering. The resource policy ship is being powered by three engines working in different directions - an impotent Commission engine, a sputtering and politically fueled Department engine and a destructive political engine.

California is not alone in this deplorable decline in responsible wildlife governance. I see various ramifications of this trend in most states, stimulated largely by special interest groups with strong political influence. These are mostly consumers of other resources who see themselves in a better position to subordinate wildlife resource protection through political avenues than through the public forum of Commission meetings. Isolating the public from resource decisions is a common strategy for these people. I see an increasing tendency to use the wildlife resource as if it were some commodity to be disposed of for private gain. Several states are engaging in depredation payments, special privileges for ranchers to take the public's wildlife, and even engaging in virtual sale or trade of the resource for monetary or political support of the government. It is amazing to me that such activities have not been the subject of more law suits filed by the public whose wildlife resources are being abused by the very agencies responsible for their protection. Unless wildlife agencies shoulder their responsibility for the resource in an honest, effective and

advocacy manner we will see more and more governance by litigation as a reflection of public frustration.

The Public Trust

Fish and wildlife are public trust resources. They do not belong to the State, they belong to the collective citizenry. In effect, the State is supposed to be the trustee for the trust on behalf of the beneficiaries, the public. Unfortunately in California, as well as in many other states, this trust status of wildlife is being ignored, not so much by the individuals involved but by the system that has degenerated into a politically-driven public relations exercise. The State has largely abandoned its trustee responsibilities. As with any trust, the beneficiaries are entitled to protection of the trust and honest, effective representation and advocacy for its continued health. The trusteeship responsibility of the trustee should be clear - it is a fiduciary relationship between the trustee and beneficiaries wherein the trustee manages the trust for the benefit of the beneficiaries. This relationship has been lost in the system currently prevailing in California.

As Australians might say, the system is "crook", meaning it is very sick. In fact, in my opinion, it is so crook, it can only be salvaged by major surgery. With respect, your Commission's laudable efforts toward "strategic planning" are, in my view, destined to fall into the category of another cosmetic exercise - admirable in intent but short of real resource protection unless you courageously recommend major corrections in the system.

The Constituency Decline

We often hear concern expressed by state fish and wildlife agencies over a decline in their "constituency". We also hear reference to this constituency as the "customers" and we see panic-driven programs rushed into being to try to shore up the support groups - the "customers". Most such programs are little more than fancy public relations exercises using a lot of impressive jargon and buzzwords to placate the public or special interest groups in the hopes of maintaining a revenue base for the current bureaucracy. I deplore the use of the word "customer" as applied to trust beneficiaries. It is demeaning to the beneficiaries and reflects either an arrogance by the agency or ignorance of the trustee duty of that agency. The wildlife resource trust is not a business dispensing a commodity for sale. Use of the word reflects the degree to which fish and wildlife agencies have lost track of their trust responsibility.

"Uncrooking" the System

The necessary major surgery to reinstate a trusteeship system could probably be accomplished in several ways but here are some suggestions:

- Establish a Wildlife Trust Commission whose members are appointed by the Governor, subject to approval of the Senate, and selected from a short list constructed by a statutorily constituted nomination board of citizens representing the trust. Said nominees to satisfy a set of prescribed experience and expertise factors rather than political acceptability. The appointees to take an oath, administered by a Justice of the State Supreme Court to uphold the trust as a trustee. The Commissioners to serve full-time and receive a salary commensurate with their service and be removable from office for failure to uphold the trustee duties. Terms of office should be staggered to ensure experience carryover and be of such length as to avoid "stacking" by any one governor.

- The Director and Deputy Directors of the Department would be appointed by and serve at the pleasure of the Commission. Their selection would be on the basis of education, professional and experience qualifications in the field of fish and/or wildlife management or research. He, or she, would also be required to take a similar oath to uphold the trusteeship responsibility.

- The role of the Department would be that of implementing the public trust management policies of the Commission. It would also serve to provide the Commission with professional advice on the status of the resource and make recommendations to the Commission regarding actions which might be beneficial or detrimental to the trust and its beneficiaries.

- The role of the Commission as an advocate, protector and manager of the wildlife public trust be set forth in the enabling legislation. Such legislation should also require that management of the trust be conducted by the Commission in open public forum with opportunity for public input.

- Rename the Commission and Department as the Wildlife Trust Commission and the Wildlife Trust Agency with the understanding that the trust includes all wild animal life, including vertebrates and invertebrates. (Some additional wording would be necessary to cover certain plants and to exclude certain categories of invertebrates) These name changes would better reflect the trust responsibility of the trustee for all wildlife, not just game animals.

These suggestions for "uncrooking" the system will be viewed in some circles as draconian, impractical or unnecessary. Most such views will probably come from special interests who wish to retain political subordination of the wildlife resource for their personal gain or by those who wish to maintain the present bureaucracy. There is an acronym that aptly describes the latter group - it is IDOUR which stands for Institutional Denial of Unpleasant Realities. Most state fish and wildlife agencies have become skilled in IDOUR.

Habitat is All Important

This presentation would be incomplete without emphasizing a most important factor in maintaining the wildlife resource. Natural habitat protection and rehabilitation are keys to wildlife resource survival. Over the years fish and wildlife agencies have been guilty of innumerable transgressions against the resource and its beneficiaries by accepting artificial or inadequate substitutes for fish and wildlife habitat. The demise of our salmon and steelhead resources and the manner in which we address endangered species problems are shining examples of this trust neglect. Such neglect is generated by both political decision-making and by the mindless view that man can always find a substitute for fish and wildlife habitat.

Without natural habitat we can kiss the resource goodbye and therefore there will be no uses, consumptive or non-consumptive. Wildlife management has degenerated into complacent, "don't rock the boat", non-trusteeship, habitat-negligent systems. They dwell on public-relation oriented exercises with ever-widening involvement in so-called cooperative or collaborative management schemes that serve largely as deceptive public placaters and vehicles for avoiding effective but politically controversial measures.

There is an ancient English quatrain that aptly describes one aspect of our negligence in protecting wildlife habitat:

> "The law locks up both man and woman
> Who steals the goose from the common,
> But lets the greater felon loose
> Who steals the common from the goose."

Our present system of wildlife resource governance encourages theft of the commons from the goose!

The Real Challenge

As I said earlier, my suggestions for "uncrooking" the system will be controversial. But, gentlemen, the present dismal outlook for the health of the resource will only worsen unless something similar is done. In my view, the wildlife resource is truly headed for extirpation under the present system of governance. Your Commission can be a courageous catalyst for change or you can continue to dabble in strategic planning exercises with cosmetic effect. You can be a champion for recognition of the trust resource for which you should be a protector and advocate, or you can drift with the tide like a jellyfish. The trust and its beneficiaries cry out for a real trustee. That is the problem and the real challenge I believe you must face.

CALIFORNIANS

DID YOU KNOW?

There is **only one** peace officer in California responsible for enforcing laws which protect fish and wildlife and water and wildlands. That classification is **"Fish and Game Warden"**.

Twenty-five years ago there were 250 of these officers in California. Now only 239 work to protect 159,000 square miles of land, more than 1,100 miles of sea coast, 3,600 natural lakes, 1,200 reservoirs and 80 major rivers. There are more than 75,000 sworn officers in the state but only 239 have the primary responsibility of enforcing laws which protect the environment. Game wardens also have statewide authority to enforce all other laws.

Twenty-five years ago game wardens were paid the same salary as a state traffic officer (CHP). **Now traffic officers make 35% more than game wardens.** (7,000 officers have a voice, 239 do not)

Warden applicants must have two years of college and a working knowledge of biological sciences, hydrology, soils, ecology and police science. **A traffic officer applicant need only have a GED.**

DO YOU CARE?

In this generation we are eradicating wildlands and species of wildlife that someday we will wish our grandchildren could just see. Much of California's water is so polluted that knowledgeable people won't eat the fish. The percentage of game law violators which are apprehended is so small as to be insignificant. The fate of California's remaining wildlife is in your hands. Act now! Demand a fair wage for the few who strive to protect **your** natural resources from the greedy and shortsighted.

Write your state senator and assembly representative today!

Ed Henke
Historical Research
769 Lisa Lane • Ashland, Oregon 97520 • 541-482-9578

April 24, 1998

Dr. Robert J. Behnke
Dept. of Fishery and Wildlife Biology
Colorado State University
Fort Collins CO 80523-1474

Dear Dr. Behnke:

Thanks so much for sharing your written words and thoughts in letter communications. I learned from each, for you are quite a few pages ahead of me in knowledge and comprehension. It really pleased me to review your historical reflections, as that's the only true way to know to what extent we've lost and how we were so successful at doing it. For those who don't look back or really care a hoot, then the conventional wisdom will continue to pay huge dividends in product on the short term, but create biological deserts on the not-so-long-term.

I think I mentioned to you that I'm completing a research presentation for advocating removal of "Matilija Dam" on the Ventura River. It will soon be finalized and you'll receive a copy. You will certainly note how history was exploited and my in-depth passion for this River and its magnificent species of Southern Steelhead.

Again, my thanks for passing along your scientific documents – and also very pleased that the article on Indian language and migrations across the Bering Strait was deemed somewhat relative to your thinking on the diverse development of other distinct individual life forms. Einstein said something about relativity, and maybe this could be a possible example of how he would relate in animate terms? At any rate, we're all thinking, and that has to be good.

Best to you.

Sincerely,

Ed Henke

From the desk of Ed Henke
HISTORICAL RESEARCH

5/8/98

DR. BEHNKE —

ITEMS I THOUGHT MIGHT BE OF INTEREST. WE HAD "RED TIDES" IN VENTURA DURING EARLY 40'S.

BEST REGARDS

Ed Henke

The Ashland Daily Tidings – Tuesday, May 5, 1998

Toxic algae kills Norway's fish

OSLO, Norway (AP) — A toxic algae is killing fish along Norway's southwestern coast, where about 400 tons of fish, mostly salmon, have been wiped out so far, officials said Tuesday.

Two research vessels are taking samples to identify the bacteria, which kills fish by clogging their gills and damaging their ability to breathe.

Selling Lake Superior Upsets Canadian Official

By David Crary
Associated Press

Toronto

The Great Lakes hold the largest supply of fresh water in the world. Yet a Canadian firm's plan to export a tiny fraction of that water to Asia is causing alarm on both sides of the U.S-Canadian border.

Foreign Minister Lloyd Axworthy entered the controversy this week, saying that Canada will try to block the proposed sale of water from Lake Superior.

"It's a matter of some real concern," Axworthy said Monday. "What we are looking at . . . is the large-scale export of fresh water, which we have always taken a strong stand against."

The furor focuses on a permit issued by the Ontario Environment Ministry authorizing a company in Sault Ste. Marie, Ontario, to pump up to 158 million gallons of water a year from Lake Superior into cargo ships for export to drought-stricken Asian countries.

The five-year permit took effect last week, although the company, Nova Group, has yet to line up any buyers.

"It's a very small amount of water . . . considering the size of the Great Lakes," Nova Group president John Febbraro said last week. "It won't affect lake levels or anything else."

Canada shares Lake Superior with Minnesota, Wisconsin and Michigan.

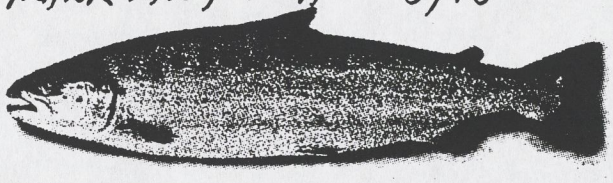
Environmentalists and politicians on both sides of the border assert that Nova Group's plan, if realized, will undermine U.S.-Canada treaties and encourage other companies to undertake larger-scale water exports.

"Water is going to become like the oil of the next century," said Sarah Miller of the Canadian Environmental Law Association. "If it's open season for all the water in the Great Lakes, wait and see what happens in the States, where there will be desperate water shortages."

Both the United States and Canada have policies that sharply restrict water diversions from the Great Lakes. Axworthy complained that Ontario did not consult federal authorities before issuing the permit.

But Ontario said it followed proper procedures, even allowing a four-week period for public comment.

FRANKLIN, N-H. 3/98



Finding Hope in a Fish Story

Return of Salmon Seen as Sign of Merrimack River's Health

By SHAWNE K. WICKHAM
Sunday News Staff

The Atlantic salmon is winning its upstream fight to return to its native waters in New Hampshire, thanks to help from one of its main predators — man.

This is the fifth year of an ambitious program to restore fishing for salmon — the "king" of sport fishing — to the Merrimack River. The brood stock program is a partnership between the U.S. Fish and Wildlife Service, which raises salmon at its Nashua hatchery, and the state Fish and Game Department, which stocks the river and its tributaries with the kind of adult fish most fishermen only dream of catching.

Approximately 3,000 brood stock salmon — averaging 8 pounds but some as large as 14 pounds — will be released this year, half this spring and the rest in the fall, according to Jon Greenwood, project leader of the Merrimack River Restoration Program for Fish and Game. Salmon season begins April 1.

Greenwood said the Atlantic salmon has a special appeal, for conservationists and anglers. "You speak to people that are reverent salmon fishermen, and there isn't another fish," he said. "I think a lot of it has to do with its mystique in terms of its complex lifestyle, its homing instinct. It travels to Greenland, Iceland, spends two years and comes back to the exact same stream it's born in.

"It's a strong fish; it's a beautiful fish. In terms of angling, it's considered the king of fish," he said.

Most people are familiar with the story of the Atlantic salmon's demise here, as a result of human progress. The

SALMON, Page 18A

Salmon Make Slow Recovery in Merrimack

SALMON
(Continued From Page 1A)

dams that harnessed river power, and the chemicals that flowed from the many mills, combined to pronounce a death sentence for anadromous fish (fish that are born in freshwater, migrate to the ocean and then return to their native waters to spawn).

Salmon, shad and herring vanished from the Merrimack soon after the first dam was built in Lawrence, Mass., in 1847, followed by other dams upriver in New Hampshire, Greenwood said. "Once the dams were built, it cut off that part of their life cycle that they needed to perpetuate themselves," he said.

There were early efforts to bring back the fish. Then, Greenwood said, "The Industrial Revolution came in so strongly, the dams were put up everywhere on the systems, and then it was really over."

The last native Atlantic salmon was caught in the Merrimack in 1896.

As recently as 30 years ago, the Merrimack was listed as one of the 10 most polluted rivers in the country; long-time Manchester and Nashua residents tell stories of watching the river change color depending on what dye the mills were using on a given day.

But then a state/federal partnership to restore habitats on the nation's rivers developed, and one program evolved into what is now called the Anadromous Fish Restoration Program. Formerly known as the Atlantic Salmon Restoration, the new name reflects a broader focus for fisheries biologists.

"We really got thinking about restoring not only salmon but other target species: herring and shad," Greenwood said.

Last year, approximately 23,000 shad came up the river, a very promising sign, he said. Herring numbers were down, largely due to natural predators, he said.

Today, the Merrimack is classified as 95 percent Class B, meaning it's safe to swim, and to eat fish caught in its waters. The utilities that own the dams are now federally obligated to provide passages to allow fish access to their breeding grounds.

That's how the Amoskeag Fishways, a popular educational facility in Manchester that boasts huge windows where the public can view salmon, shad and other species each spring, came into being. This year's fish season runs from May 4 through June 14. An estimated 20,000 people are expected to visit during that six-week period, and the Fishways is open 7 days a week.

Amoskeag Fishways is owned by Public Service Company of New Hampshire and managed by Audubon Society of New Hampshire, in cooperation with Fish and Game and the U.S. Fish and Wildlife Service. Among its educational programs is an annual four-part monthly series for school children on the lifestyle of the Atlantic salmon.

Tom Desrosiers, an Audubon program naturalist who works at the Fishways, said it's important to educate the public about the Atlantic salmon, and its role in the health of the river habitat. "It's a bio-indicator, which means without this, chances are something is wrong with this eco-system," he said.

Desrosiers said Atlantic salmon are still unable to reach their historic spawning grounds here, the tributaries of the Pemigewasset, Baker and Piscataquog rivers, among others. The salmon you'll see in the Amoskeag Fishways window during fish season are brood stock salmon, put there so the public can learn about and appreciate these fish.

On rare occasions, a wild salmon has made its way into the fish ladder, he said, and can be distinguished easily by its lack of a tag and scarred appearance. "It looks like the fish has gone through hell and back," Desrosiers said. "Darwin's finest."

For now, Merrimack River anglers will have to rely on the brood stock fish, adult fish that have been stripped of their eggs and then released by Fish and Game officers into the river.

"This is one of the few places people can go to catch Atlantic salmon, other than Newfoundland and parts of Quebec," said Eric Aldrich, programs information officer for Fish and Game.

Greenwood said Fish and Game released about 1,000 brood stock fish last fall around the Eastman Falls dam in Franklin; those fish will have dispersed and found their own territories along the river. Another 1,500 will be released this spring, beginning in a couple of weeks — just in time for the start of salmon season, which runs from April through September.

According to Fish and Game figures compiled last week, 1,989 anglers bought $10 permits to fish for salmon last year (required in addition to a regular fishing license). A Fish and Game survey, compiled from the fishing diaries anglers are asked to fill out, found an estimated 68 percent of those actually fished. And nearly one-third caught salmon.

On average, it took 14.6 hours to catch a fish. And the average angler spent $110, for a total of $148,720 spent on salmon fishing in 1997.

Greenwood believes federal and state resource managers have a special responsibility to restore native species. "The whole national theme is we should be working with our native population and trying to do the best we can for them," he said.

Desrosiers said his fascination with the Atlantic salmon is professional and personal. "I have so much respect for a fish that can leap 12 feet through a waterfall, that can survive hundreds or thousands of predators, both natural and human ... It's kind of spiritual."

"It's just a symbol of life, really. It demands respect."

Five years into the brood stock program, Segarich declared it a "great success."

"We have fishermen coming from all over New England and even down from Canada to go fishing here. Right now it's the largest Atlantic salmon fishery in New England," he said.

For anglers who live here, he said, it's a chance of a lifetime. "They have the opportunity to do things that 10 years ago they would have to go to Canada to do."

Helping Salmon Make the Trip

From Staff Reports

Some of the brood stock salmon being caught in the Merrimack River in New Hampshire are adult fish that have been captured by federal biologists at a dam downriver in Lawrence, Mass., each spring.

These fish, survivors of a two-year roundtrip from their native streams to the northernmost ocean and back again, are brought to a federal hatchery run by the US Fish and Wildlife Service in Nashua. There, in the fall, adult fish are stripped of their eggs, most of which will then be raised into fry (young salmon) at a state hatchery in Warren.

Victor Segarich, manager of the U.S. Fish and Wildlife Service hatchery in Nashua, said currently there are not enough wild fish returning to the Merrimack to provide sufficient diversity in the gene pool. So biologists acquire additional stocks from Maine to supplement the wild fish eggs.

Each year, some eggs are kept at the Nashua hatchery, where the salmon are raised in captivity until they are ready to spawn at age three or four years. These fish, and those caught in Lawrence, are the brood stock fish for the coming salmon season.

As for the eggs hatched in Warren, folks from Fish and Game, the Fish and Wildlife Service and volunteer conservation groups stock some three million fry from the state hatchery in streams all over New Hampshire.

Eventually, these fish will leave their freshwater home and head for the ocean. Then, like their ancestors, those that survive predators and manmade hazards will head back up the Merrimack. Those that make it to Lawrence — only 71 last year — will be captured and taken to Nashua for harvesting, completing the cycle.

The adults that provide the eggs now are ready to be released. And for five years, that has meant a boon for anglers.

Segarich said the main impetus, and reward, for all the hard work is "just to know we're bringing back a fish that has been extinct for 100 years."

THE MAIL TRIBUNE • SATURDAY APRIL 18, 1998 • ALA CARTE • APRIL 21, 1998

Precocials make for quite a catch

By MARK FREEMAN
of the Mail Tribune

Local lakes and ponds will be stocked with young male steelhead that have matured rapidly, and they can be caught and kept as trout.

The fish are called "precocials" because they sexually mature too early to survive a trip from Cole Rivers Fish Hatchery to the ocean like normal hatchery fish.

The Oregon Department of Fish and Wildlife plans to stock up to 23,000 of these overdeveloped steelhead in eight local ponds and lakes.

The 8- to 10-inch fish are great finds for local anglers, who get to keep the small steelhead that fight and taste like their older, larger cousins.

Precocials are a phenomenon of the hatchery.

Male steelhead fry in hatchery ponds occasionally grow and mature faster than normal and end up sexually mature at about a year old.

Hatchery workers find these fish by squeezing their sides, which sends milt, or fish sperm, flowing from the bodies as if they were a male adult in the middle of spawning.

Biologists suspect that the rapid development of some fish is because most of the fish food at hatcheries is ground-up fish carcasses. These carcasses contain far more of the male testosterone hormones than the food steelhead get in creeks and rivers.

The local precocials all come from Cole Rivers, near Trail.

Here is the ODFW's precocial steelhead stocking schedule:

- Expo Ponds — 4,000.
- Denman Ponds — 2,600.
- Burma Ponds — 600
- Spaulding Pond — 600.
- Dutch Herman Pond — 600.
- All-Sports Pond — 600.
- Fish Lake — 5,000.
- Emigrant Lake — 3,000-6,000 (depending upon how many are left over).

THE MAIL TRIBUNE • SATURDAY APRIL 18, 1998 • ALA CARTE • APRIL 21, 1998

Fish to feast on rich diet

Project to put carcasses on table for coho

By MARK FREEMAN
of the Mail Tribune

The World Wildlife Fund is paying $25,000 to Oregon Trout for a two-year project that will place dead coho salmon in key spawning tributaries used by native coho.

Nutrients from the decaying fish will help create a better underwater environment for infant salmon to feed on.

Studies done in British Columbia as well as by the Weyerhaeuser Co. and the U.S. Forest Service show that nutrients from carcasses help grow bigger, healthier salmon smolts. Strong smolts have a better chance of surviving to adulthood.

"The uptake is incredible," says Steve Hinton, who is running the project for Oregon Trout. "It all correlates to better fitness, better survival of smolts."

The Oregon Trout project recently won the annual Walter A. Haas Jr. Conservation Award grant, which is administered by the World Wildlife Fund.

It's the second of 10 annual grants in the name of Haas, the former Oakland A's and Levi-Strauss Co. owner who often vacationed and fished the Rogue. The Haas family owns the former Zane Grey cabin in the Rogue River Canyon.

For the past seven years, Hinton has pursued carcass stocking as a way to improve the amount of "marine-derived nutrients" in streams. These nutrients support the lower aquatic life on which infant fish feed, Hinton says.

With drops in wild spawning adults, such nutrients have been missing from many streams — thereby exacerbating problems wild fish encounter, he says.

State water-quality laws have always outlawed the unchecked placing of fish parts in creeks, but the state Department of Environmental Quality has relaxed some of those standards for study projects.

The laws are in place because too many nutrients in streams cause algae blooms that suck oxygen out of water and actually harm fish, says DEQ engineer Jon Gasik.

But the DEQ is working with the Oregon Department of Fish and Wildlife to improve nutrient-poor streams, Gasik says.

"It's crazy that we've had to jump through so many hoops to put some carcasses out," Hinton says. "It was laughed at. Now, it's the missing link."

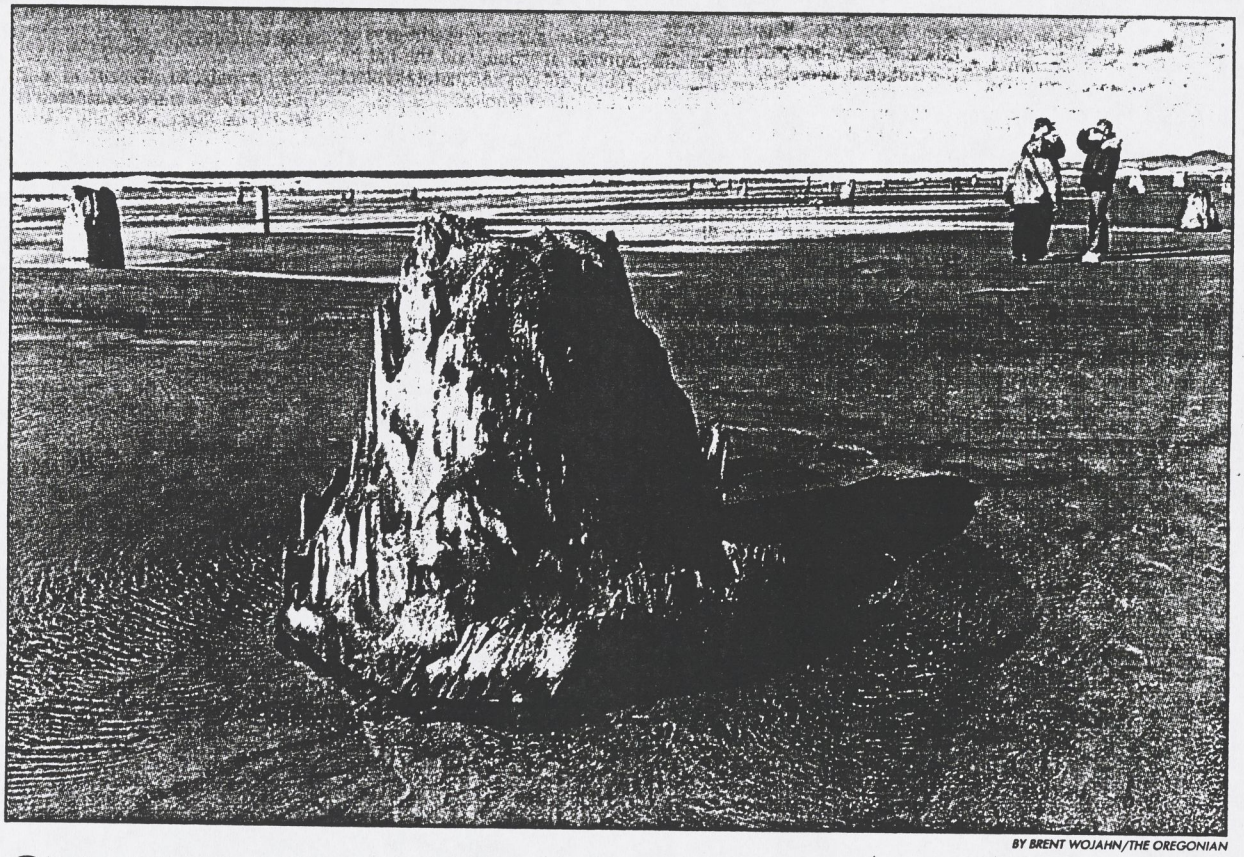
Oregon Trout will do analyses and surveys in late summer to find three test creeks and one control creek for the study. The carcasses will be placed in the creeks for the next two winters.

Cole Rivers Fish Hatchery, which has thousands of excess hatchery coho adults annually, will supply the carcasses. The fish will be killed at the hatchery and frozen, then given to Oregon Trout for planting in the streams. Volunteers will put the fish on stringers and place them near log jams during winter freshets, Hinton says.

Oregon Trout will study how many infant salmon and steelhead those carcass-stocked streams produce compared to the unstocked streams, Hinton says.

San Francisco Chronicle THURSDAY, MARCH 12, 1998

El Niño Digs Up Ancient Forest



BY BRENT WOJAHN/THE OREGONIAN

Giant tree stumps at the beach near Neskowin, Ore., unearthed by El Niño storms, gave beachgoers a look at the remnants of a forest that stood 2,000 years ago. This winter's storms have stripped 10 feet of sand off the beach and exposed more than 200 of the 3-foot tall stumps. Scientists believe an earthquake 2,000 years ago dropped the coastline up to seven feet and submerged the trees. The stumps have been visible since mid-February, but ocean currents are expected to rebury them by summer.

CONTEXT INSTITUTE

*PO Box 946, Langley, WA 98260 * Tel: 360/221-6044; Fax: 360/221-6045*

Since its founding in 1979 by Robert and Diane Gilman, CONTEXT INSTITUTE has explored how human society can become sustainable (i.e. able to meet the needs of the present without diminishing the prospects for the future), and has served as a catalyst for voluntary change toward a more humane and sustainable culture. We are one of a handful of organizations that have focused on sustainability as a central theme for more than a decade, and we are now internationally recognized as an authority in this area.

We are best known for our journal, *IN CONTEXT: A Quarterly of Humane Sustainable Culture.* in print from 1983 to 1995 and now continuing on this site. We are also involved in a variety of other publishing and collaboration & consulting programs.

The Institute, an independent non-profit (501(c)(3)) organization, was initially a local living-lightly organization. In 1983, we began our quarterly journal and broadened our focus. In the succeeding years, Institute staff have published, spoken, and consulted in such diverse areas as community development, cultural history and cultural change, systems thinking, education, ecological living, sustainable economics, and the built environment.

Central to our approach is our sense that the world is now going through a process of cultural change that is as profound as the shift, over 5000 years ago, out of hunting and gathering and into agriculture and cities. We refer to that previous shift as going from the Tribal Era to the Empire Era. We see ourselves as now in the transition between the Empire Era and the Planetary Era. (For more detail on this perspective, see "What Time Is It?".)

We recognize the great dangers of our times, yet, because the underlying momentum of change is so great, we also see these as times of great opportunity to develop humane and sustainable cultures for the Planetary Era, cultures that could provide a quality of life for all that would make today's societies look like the dark ages. It is this positive vision of the possible, together with a keen awareness that time is running out, that motivates our work.

While we address some of the same issues as those addressed by environmental, political, social-action, and personal-growth organizations, our approach is different. As much as possible, we approach these issues from the context of the emerging Planetary Era, rather than within the context of the waning Empire Era. This leads us to focus on *yes* rather than *no*, on *voluntary human-scale innovation*, and to integrate the full gamut of human concerns environmental, social, economic, personal into a long-term, whole-system, constructive perspective.

Much of the Institute's work focuses on encouraging the sustainable redevelopment of the industrialized world (i.e. the rich countries of the North plus their many cultural extensions throughout the world). We focus here because we feel that most of the world's unsustainable practices have their roots in these globally dominant societies. Any real solutions must address, and help to transform, this cultural core. Indeed, we feel that such sustainable redevelopment, with all the profound cultural change that will entail, is *the* central challenge and task facing the industrialized world, and humanity, during the coming decades.

The organization directs its work towards those who are willing and able to help move their organizations, their communities, their personal lives, and their societies in a more humane and sustainable direction. We think of these people as cultural leaders, some of whom are in positions of

institutional power, and others who are simply influential through their own initiative and sensitivity. We focus on these early adopters because experience shows that the most effective way to promote lasting cultural change is to educate and empower cultural leaders who then influence the rest of society.

We assist these cultural leaders through a variety of programs which enable them to discover:

- a whole-system understanding of the new human ***context*** at the dawn of the 21st century
- practical, experience-based ***approaches*** to the perplexing issues of our times consistent with this emerging context
- ***strategies*** and ***skills*** for effective change
- realistic ***vision***, ***hope*** and ***empowerment***

In addition to expertise in particular topic areas, our work is characterized by a way of thinking which we feel is important for the development of humane sustainable cultures appropriate for the Planetary Era. While there is no simple name or description for this way of thinking, it includes the following elements:

Systems Thinking - We draw on our background in systems theory to ask and help those we serve to ask: How do the pieces in the puzzle fit together? What's going on beneath the surface? What are the significant feedback loops that tie a system together? What are its dynamics in time? At what points in a system can change most fruitfully be introduced?

Solution Orientation - We start where many others leave off: with a vision of a preferred future (humane and sustainable) and a critical awareness of the problems of the present. With this as our starting point, we see our *primary* task as searching for those constructive, experience-based, promising solutions and approaches that could provide a path from today's problems to that preferred future. While others provide the necessary "no" to the dysfunctions of business-as-usual, we focus on providing the necessary "yes" that provides a viable and desirable alternative.

Ecological Thinking - Our ability to survive as a species requires an understanding of human interdependence with each other and with all life and a recognition that we must find solutions that work for the whole. The ecological system is both the basic reality in which we need to function and a fruitful metaphor for more sustainable human systems, such as production systems in which the wastes from one process become resources for another.

Long-Term Orientation - A deep sense of history, going back thousands, millions and even billions of years, helps us to more richly understand the character and possibilities of cultural evolution. A long-term commitment to many generations into the future provides the moral foundation for the basic principles of sustainability. Taken together, they enable us to focus on essentials and avoid being distracted by the fads and short-term news of the day.

Compassion and Forgiveness - We are all in this together. We are all a part of, and to varying degrees collude with, the unsustainable systems in which we are embedded ... *and* we all have something to contribute toward a positive future. Context Institute is committed to a clear-eyed understanding of the problems of today, but we are not motivated by an interest in finding individuals or groups to blame. We work instead to remind ourselves and each other of that more spacious spirit in which compassion and forgiveness are natural responses, and healing is the natural result.

By applying this way of thinking to a wide variety of social, cultural, and ecological issues, we have helped with the building of vision for a sustainable future among a small but influential group of opinion leaders and innovators. We intend to continue to extend the range of people involved in exploring these

issues and building this vision.

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CALIFORNIA TROUT
KEEPER OF THE STREAMS

Streamkeepers Log

ENTRY NO. 84 | TWENTY-SEVENTH YEAR | SPRING 1998

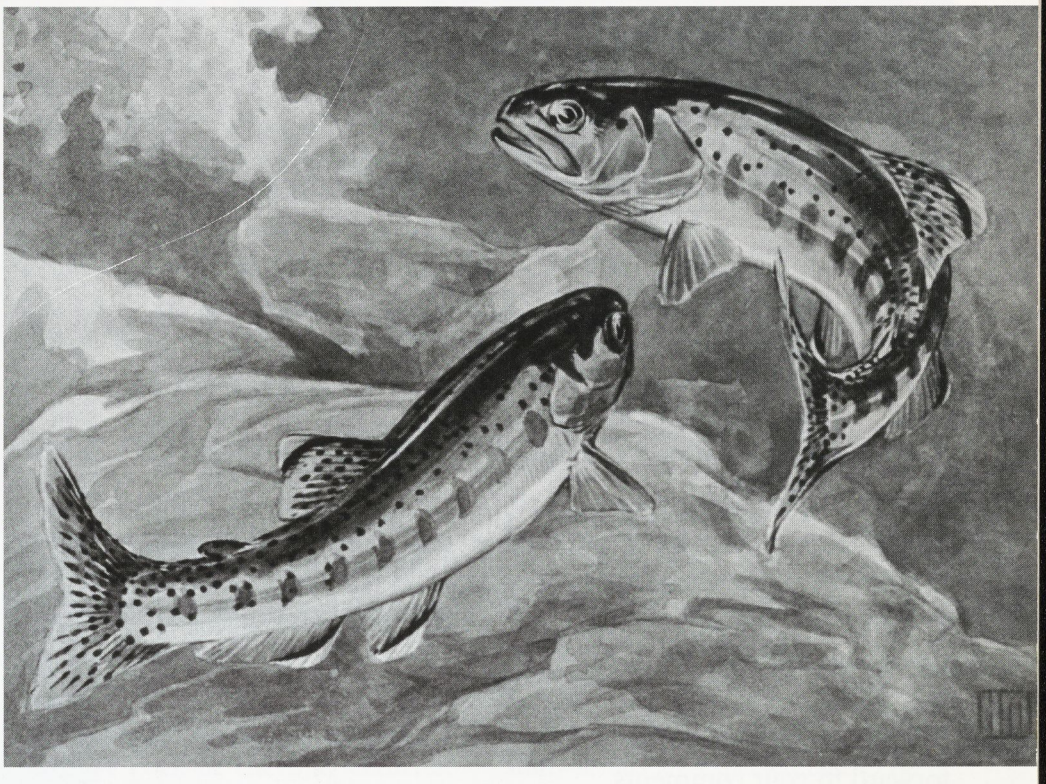
WILD TROUT PROGRAM
Heritage Program
Cottonwood Lakes
Genetic Testing

THE PUBLIC TRUST
F&G Commission
Exotic Species

STEELHEAD PROGRAM
ESA Listing

HYDRO REFORM
Santa Ana River
Eel River

SPECIAL FEATURE
A River Remembered



California Gold

CALTROUT PROPOSES HERITAGE PROGRAM

Twenty-seven years ago, California Trout appeared before the California Fish & Game Commission with a bold new proposal. Why not, we asked, augment the State's hatchery program with a new program designed to manage State waters for wild trout? The proposal included special regulations crafted to protect and enhance existing wild trout populations statewide.

(Continued on page 14)

Editorial

SPRING FORWARD

Spring brings another trout season, but the 1998 season brings something different for CalTrout members—a new look.

This isn't easy. The Log has been relatively static for a quarter century, establishing an almost Wall Street Journal-like familiarity. So why the change?

CalTrout recently completed a major strategic planning process which identified, among other things, a crucial need to convey our message more effectively. Whether winning new friends, or debating foes, the future of our work depends on getting our message out. Thus, the need for upgrading the Log.

Staff and graphic designer Jeff Bright teamed up to provide a new format for the Streamkeepers Log. In this, and future Logs, look for more pictures, better graphics, and a layout tied more closely to the areas outlined in our Strategic Plan. You will also find a new and attractive layout at our website, also a product of teamwork between Jeff, Webmaster Larry Davidson, and staff.

We hope you enjoy CalTrout's new "look," and we look forward to your comments.

On the cover: 1939 painting by Hashime Murayama.

CALIFORNIA TROUT

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Ed Henke with a "brace" of steelhead taken during the summer of 1946 in the Ventura River above the Foster Park Bridge. *Jack Gruell photo*

I think that should be three brace of steelhead.

Fishing for Science

GENETIC TESTING OF SOUTHERN CALIFORNIA RAINBOWS

When a rainbow trout tops 10 pounds, most anglers know they've hooked a steelhead. But in the headwaters of many Southern California streams, where anglers find colorful but diminutive rainbows, identification can be less apparent.

Trout found high in the mountains of the Angeles, Los Padres, and Cleveland National Forests are colorful, but their heritage is about as mysterious as the notion of wild trout in Southern California.

Controversy over their heritage was generally limited to the casting ponds, until last August, when Southern California steelhead were classified as endangered under the Endangered Species Act. Speculation about the genetic makeup of the stunning SoCal rainbows peaked, and the controversy has continued to this day.

In order to solve this mystery, CalTrout and the Southwest Council of the Federation of Fly Fishers (FFF) will conduct a genetic sampling and testing project. This Spring, eager volunteers armed with fly rods and luck will set out to catch trout from the East Fork of the San Gabriel. Once in hand, the trout will be subjected to small fin clips as tissue samples, and will then be released to continue their adolescence. Study results should demonstrate whether growth will stop at the 10 inch or 10 pound mark.

Many anglers of the area believe that the wild rainbows populating the headwaters of rivers throughout the area are related to steelhead. They are disturbed that the listing neglected these isolated populations. Resource managers have countered that these trout are hatchery fish and warrant little, if any, special attention.

The tissue samples will be shipped to Dr. Jennifer Neilsen, a geneticist who specializes in the heritage of California's trout and salmon populations. DNA markers have proven to be compelling evidence for the purpose of identifying a fisheries lineage, and were critical to the endangered species listing for Southern California steelhead. The study results are expected late 1998.

Findings could lead to a variety of conservation strategies for the region's wild trout. If related to steelhead, these headwater populations could prove instrumental to recovering SoCal Steelhead populations. If they're a unique strain of coastal rainbow, other protective measures might be warranted.

WILD TROUT *Program*

Historical Footnotes

COTTONWOOD LAKES EGG-COLLECTING STATION

During the summer of 1917, preliminary surveys were made of the Cottonwood Lakes area in Inyo County to ascertain whether it would be feasible to undertake the propagation of golden trout.

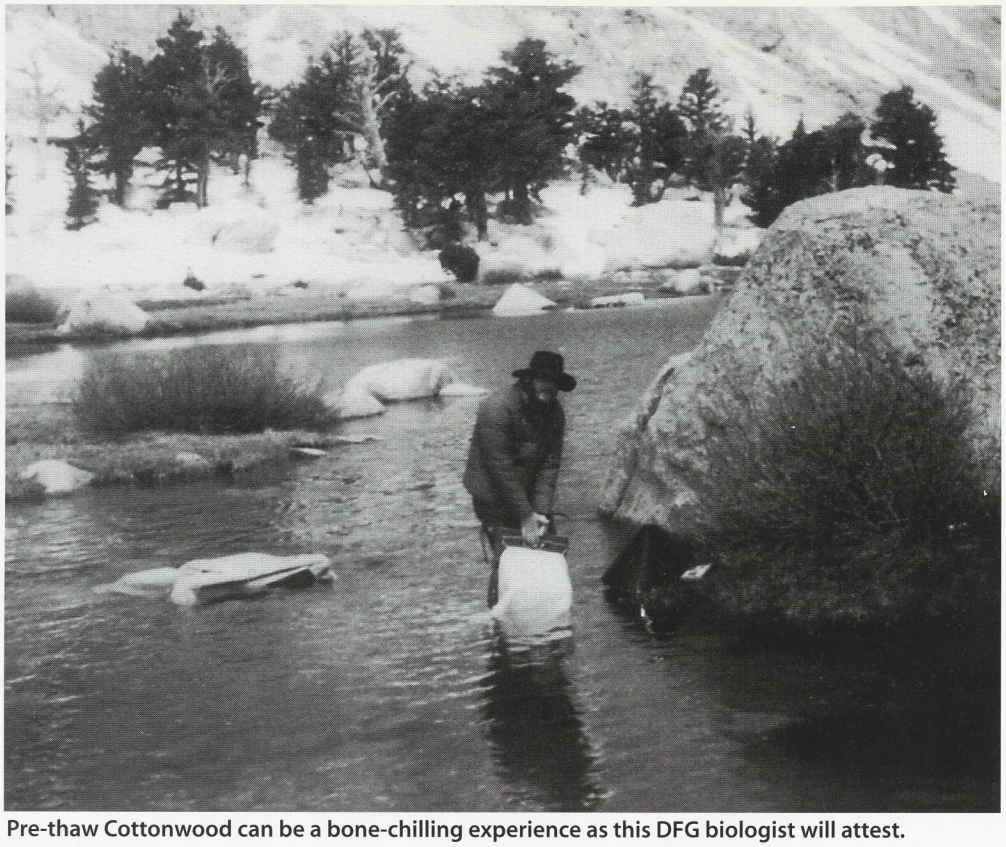
The Cottonwood Lakes are situated in a rugged, almost inaccessible section of Inyo County near the Tulare County line, at the head of Cottonwood Creek, at an elevation of 11,150 feet. The lakes were stocked in the early 1870's with golden trout from Mulkey Creek, a tributary to the South Fork Kern River.

The remoteness of the site from railroads, highways, or human habitation, the high altitude, and severe weather conditions make the trip during the spring months a hazardous undertaking. Nevertheless, the work has been continued and crews have gone into the lakes many seasons to obtain golden trout eggs.

MT. WHITNEY HATCHERY

Often referred to as "The Stone Monument," the Mt. Whitney Hatchery was constructed in 1917 and still plays an important role in California's hatchery program.

To indicate their interest in the hatchery and assure its establishment at Independence, local citizens called a meeting and solicited public donations for purchase of the hatchery site. The drive for funds netted $1,850 in cash, $1,500 of which was used to purchase the 40 acre tract on which the hatchery is located. Built of native granite boulders, and of pleasing design, the hatchery is quite impressive. It has withstood the rigor of the seasons since 1917.



Pre-thaw Cottonwood can be a bone-chilling experience as this DFG biologist will attest.
photo courtesy of Jim Yarbrough, Mt. Whitney Hatchery

Once in a Lifetime

COTTONWOOD LAKES OPENED TO FISHING

For decades, the California Fish & Game Commission jealously guarded their golden trout broodstock in the Cottonwood Basin outside of Lone Pine. Now, thanks to decades of good management, anglers can soon enjoy unparalleled angling for golden trout in the High Sierra.

WILD TROUT

The DFG has determined that golden trout populations in the Cottonwood Lakes are sufficiently abundant to allow catch-and-release fishing without risk to the hatchery program. Based upon a recommendation from the DFG, the Fish & Game Commission adopted an open season starting in 1998, extending from July 1 through October 31, and including a zero bag limit, and single, barbless, artificial lure restrictions.

"Anglers have a chance to fish in a

High Sierra 'hatchery' with a real shot at catching trophy goldens exceeding two pounds," said Jim Edmondson, Executive Director of California Trout. "This is a great move by the DFG to expand fishing opportunities through creative and protective management."

For decades the golden trout of the Cottonwoods Basin have been used to stock High Sierra waters. For many years the fish were transported in by mule train. More recently, aerial plants have been the preferred method.

To the surprise of many, CalTrout and a host of Eastern Sierra interests forestalled a 1994 attempt to close the Mt. Whitney Fish Hatchery, arguing that the historical and biological value of the hatchery far exceeded the potential savings gained by closure.

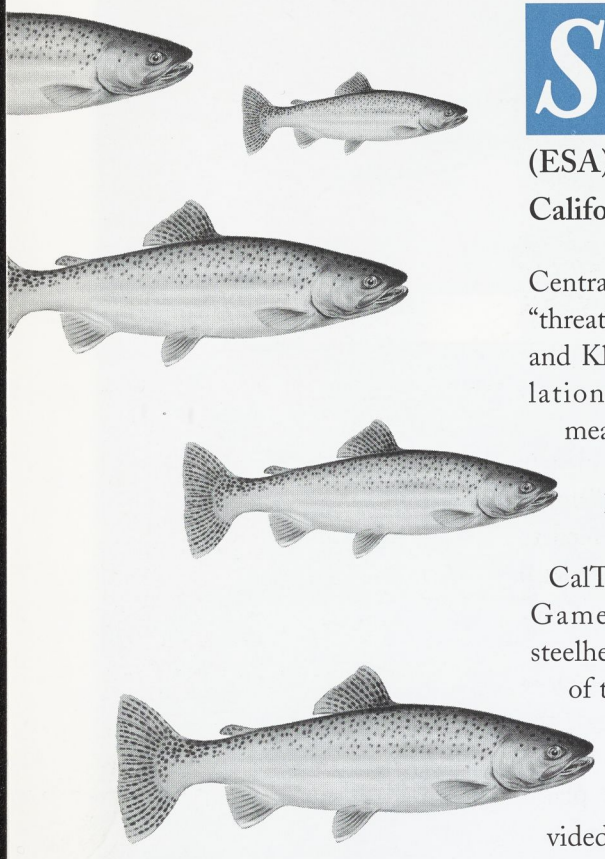
The Mt. Whitney Hatchery is the sole source of golden trout in the world.

Top: **Mt. Whitney fish hatchery near Lone Pine, California, circa 1920's**
Middle: **Hatching tanks inside Mt. Whitney**
Bottom: **Egg-collecting station**
photos courtesy of Eastern California Museum

Program

Lukewarm Applause

ANGLERS GREET STEELHEAD LISTING WITH HEALTHY SKEPTICISM



San Francisco– Friday, March 13. Following extensive delays, the National Marine Fisheries Service (NMFS) narrowly avoided contempt of court charges by issuing a final Endangered Species Act (ESA) ruling on steelhead trout populations in the Central Valley, Northern California, and Klamath Mountain Province regions.

Central Valley populations were listed as "threatened," while Northern California and Klamath Mountain Province populations received "candidate status," meaning they are not formally listed, but may be added to the ESA list at any time.

CalTrout convinced the State Fish & Game Commission to extend the steelhead season through March as part of the State's emergency angling regulations. The weather proved less flexible. A very wet El Nino winter provided few fishable days.

NMFS's long-awaited decision came in response to a series of court orders brought about by conservationists frustrated with the federal government's past failures to meet the ESA listing guidelines. When NMFS failed to meet their February 9 deadline for a decision, a group of conservationists sought relief in court.

On February 13, Judge Susan Ilston of the US District Court, Northern District, ordered a March 13 deadline for a NMFS decision. According to the order, if NMFS had failed to meet their deadline both NMFS Director Rolland Schmitten, and his immediate supervisor, Secretary of Commerce William Daley, would have faced contempt of court charges.

"We're relieved that NMFS has made a final determination on the listing," said Steelhead Program Leader, Tom Weseloh, "...but too bad we had to sue the federal government to do their job."

In a curious twist to the Central Valley listing, NMFS chose threatened rather than endangered status, despite critically low population levels, and little available habitat. This decision was based on a "strong CALFED process," an argument citing the joint state-federal process which is currently seeking a solution to Delta water quality issues.

Recovery plans accompany the listing. While they could go much further, they will be complemented by funds now available from SB 271, Senator Thompson's (D-St. Helena) bill which

STEELHEAD

Report Card

In our last issue, we highlighted CalTrout's Steelhead Program; a list of objectives of highest priority for recovering steelhead populations statewide. Concurrent with the listing of Steelhead under the Endangered Species Act, CalTrout has engaged in extensive discussions and negotiations with resource agencies in an attempt to obtain as many of our priorities as possible. The State and the Feds have signed a Memorandum of Agreement on the provisions for steelhead recovery, and many of our requests are incorporated within that MOA. The following represents what we wanted, and what we got.

(continued on page 7)

Steelhead? The Trinity River supplies beautiful scenery and, hopefully, the fish.
John Nordstrand photo

provided $43 million dollars for steelhead recovery programs over the next ten years.

The listing includes a provision to review the Forest Practice Rules, and *possibly* modify them. This is watered-down policy, but provides steelhead fans a forum to make their concerns known.

D Program

California's steelhead populations have declined 90% since the 1950's. According to C.F. Raysbrook, a senior official at the Department of Fish & Game, "...the major factor causing the steelhead population decline is freshwater habitat loss and degradation."

Anglers, who bare the brunt of recovery through restrictive angling regulations, view the listing with skepticism. They express concern that although state and federal resource agencies have clearly identified the causes of the declines—habitat degradation—they have failed to utilize the ESA, or any other existing legal regulations, to improve habitat conditions.

Nevertheless, with respect to recovery plans, the proof is in the pudding. If the state can effectively mobilize to implement the recovery plans, the listing will provide a much needed boost to recovery efforts.

"NMFS and California's Department of Fish & Game are hanging in the balance now," says Edmondson, continuing, "...they can either remain afraid to follow their own science to alleviate the habitat degradation that has caused the decline, or they can step up to the plate and start the hard work of recovery by aggressively implementing their own recovery plans."

Edmondson said, "This decision sounds the bell for the first round of a ten-round fight."

(from page 6)

CALIFORNIA STEELHEAD PLAN

The Plan is now off the dusty shelf. In general, its provisions are incorporated in the MOA. Efforts to fund the Plan are now under way through the State budget process. More later. The only downside; still no summer steelhead component to the Plan.

HATCHERIES

Here we got just about everything we wanted, except for genetic testing.

- ✔ Mass Mark Steelhead
- ✔ End Sub-Smolt Releases
- ✔ End Inter-Basin Transfers of Fish

MONITORING/STOCK ASSESSMENT

Here again, as part of the MOA, we got just about everything we wanted. Mass-marking is under way, and with regards to monitoring and establishing baseline population estimates the State must, by May 1, 1998, implement a process for setting recovery and strategic goals for naturally spawned North Coast Steelhead, and initiate a monitoring program to measure hatchery fish stray rates on North Coast steelhead spawning grounds. By June 1, 1998 the State must develop a comprehensive monitoring program for North Coast steelhead to comprehensively assess the health of North Coast steelhead populations.

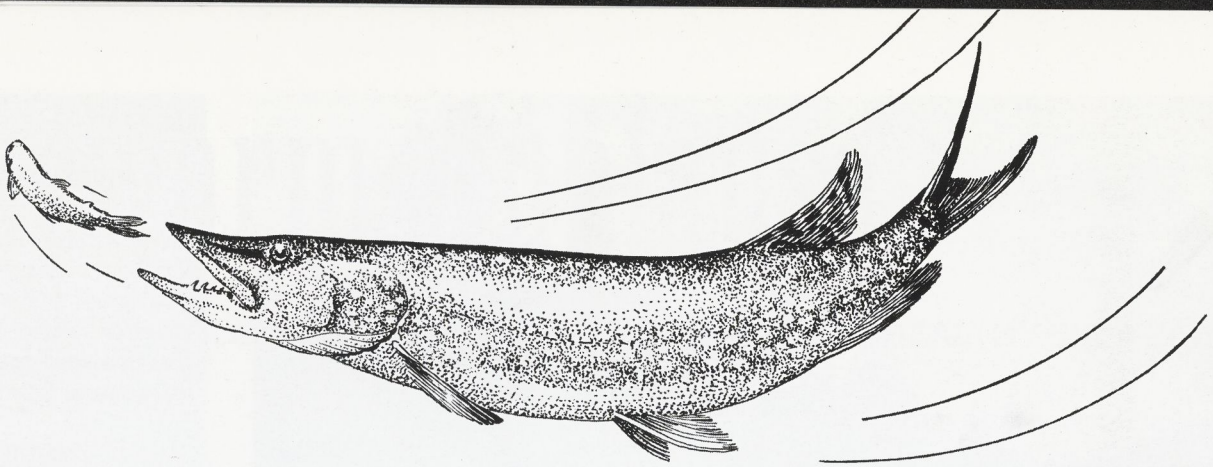
- ✔ Determine Hatchery vs. Wild Component
- ✔ Conduct Spawner Surveys
- ✔ Conduct Downstream Migrant Trapping
- ✔ Set Population Goals

ANGLING ISSUES

As you may have noticed, stringent angling regulations accompanied the steelhead listing. These may be revised pending the assessment of steelhead populations by the DFG. CalTrout supports and, in fact, helped develop the current angling regulations.

Steelhead Catch Report/Restoration Card
We didn't get anywhere with this one, but hope to in the following year. More later.

- ❑ Increase Price/Lower Overhead
- ❑ Add Hatchery/Wild Identification Box
- ❑ Add Mechanism To Monitor Bag Limits
- ❑ Mandatory Return/Analysis Of Cards



Bucket Biologists Beware!

CALTROUT DEVELOPS LEGISLATION TO MAKE THE FINE MATCH THE CRIME

When the Department of Fish & Game (DFG) started the environmental documentation for ridding Davis Lake of invasive and destructive northern pike, they thought the hardest part of the job would be destroying the pike. They were wrong.

Compared to the public relations firestorm the DFG weathered over the program, removing the pike was a cinch.

"The program just caused a lot of division and soul searching within the fisheries and environmental communities of California, not to mention a big price tag for taxpayers," said CalTrout governor Pete Giampaoli, a resident of Chico.

Controversy was the order of the day, but what most new reports failed to mention was that no matter where you stand on the issue, the perpetrator's punishment (assuming we could find him) would be little more than $1,000 in fines.

To make the fine fit the crime, Giampaoli has worked closely with an attorney to draft a new bill providing a substantial punishment for introducing non-native fish and other aquatic species into California's waters.

AB 1625 has been introduced by Assembly Member Bernie Richter (R-Chico). It is patterned after the "arson law," laws requiring that persons responsible for starting a fire pay the costs to put out the fire and restore the damage.

While the current Fish and Game Code makes it a crime to place or plant in the State waters any live fish, any fresh or salt water animal, or any aquatic plant without obtaining permission from the Department of Fish and Game, AB 1625 steps up the pressure a notch.

The PUBL

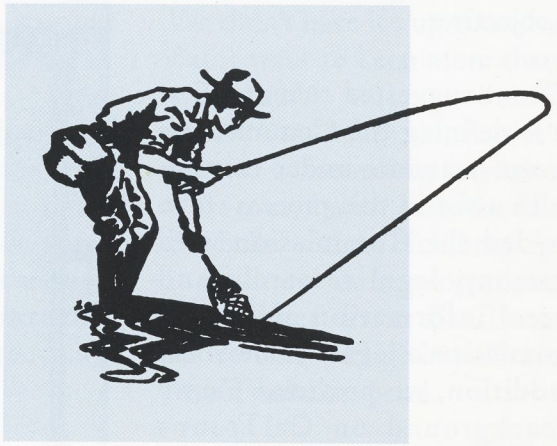
Under AB 1625, any person who violates the current Fish and Game Code with threatening, non-native species is liable for the damages to property caused by the violation. The person is liable for all monetary damages caused to any commercial or sport fishery or to the public communities that depend upon those fisheries for their income.

What's more, AB 1625 would make this violation a felony with up to 5 years imprisonment, provide a minimum fine of $20,000, revocation of the defendant's state fishing privileges for five years, and

Despite the smile of this ardent biologist, elimination of a non-native species is never a pleasant job. Shown here, piscine carnage from the 1960's Hat Creek squawfish eradication. *CalTrout file photos*

provide a reward of $50,000 payable to persons providing information leading to a conviction. This

BLIC TRUST



provision is sure to pay off when bar-room braggarts and other bucket-biologists regale their friends with tales of their deeds.

Despite all the controversy over the Davis Lake rotenone treatment, here is a law and order provision which all Californians can rally behind.

Under the direction of CalTrout volunteer Nick Di Croce, Trout Clouters will soon organize a letter-writing campaign in support of the bill. For more information, contact Nick at (310) 543-1877.

Stay Tuned for Mission Identification

COMMISSION DEVELOPS STRATEGIC PLAN

Responding to charges that they have become a rudderless ship of state, the California Fish & Game Commission has launched a strategic planning process to help them do their job better. The process began in December, and CalTrout was invited to participate in the process.

"CalTrout has a vision, and we want you to help us sharpen our focus," said long-time Commissioner Frank Boren.

The PUBLIC TRUST

Rarely in recent memory has the Commission been filled and staffed by so many thoughtful individuals willing to take a broad look at the Commission's goals and objectives.

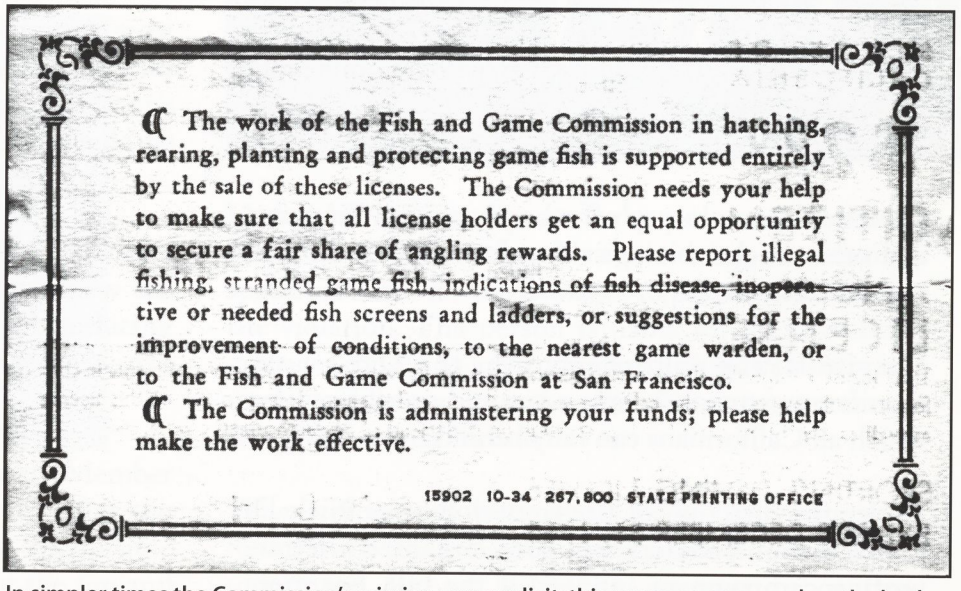
CalTrout suggested that the first step is defining the Commission's role and mandate under existing law. To assist in this process we've provided the Commission with testimony, legal research, and general information about the Commission's legal framework. In addition, we provided plenty of background on CalTrout's vision for resource protection in California.

CalTrout believes that the Commission is empowered to supervise the Department of Fish & Game, but since being re-organized in the early 1950's, has been effectively prevented from doing so. Since the Commission has few staff members, none of whom are biologists, Commissioners rely on the advice offered by the DFG.

Unfortunately, the top tier of the DFG is staffed entirely by political appointments, so the message the Commission hears typically emanates from the Governor's office, not from the trained staff within the DFG.

Ironically, the Commission has one of the strongest constitutional mandates of any California agency, but due to staff and funding limitations is frequently unable to exercise its authority.

Perhaps the strategic planning process will move the Commission forward into a new era for California's fish and game.



In simpler times the Commission's mission was explicit; this message appeared on the back of a 1936 fishing license.

A Founding Member Remembers

DAYS ON THE NORTH FORK FEATHER

Old-timer Larry Rankin doesn't fish much anymore…he's nearly eighty, and wading the Pit isn't on his to-do list these days. But that doesn't bother Larry in the least. He's had some of the best fishing that many of us can only dream about.

Larry grew up in San Francisco, went to Galileo High School when sandy roads and horse-drawn cable cars were all that took visitors out to the Beach. His Boy Scout troop, Troop 14, was led by another San Francisco native, Richard Goldman. Every year the troop gathers for a reunion, although, as Larry says, "…it's getting harder and harder to fill a table."

When wire-drawn harnesses carried people into Yosemite Valley, Larry was there, working as a summer caretaker. Years later, the day before they flooded Trinity Center with Claire Engle Dam, Larry drove through, one last time, "just to remember what it looked like."

And from 1928–1936, Larry fished the North Fork Feather River with a passion that few other rivers in the West deserved.

> *"The Gods do not deduct from man's allotted span the hours spent in fishing."*
>
> –Babylonian Proverb (often quoted by Herbert Hoover)

This was before chain gangs out of San Quentin built the highway up the canyon, so getting there wasn't a Sunday picnic.

"The Western Pacific ran a daily train from Alameda, up through the canyon. There was a little store at Gray's Flat, and you had to tell the conductor to let you off there. Then, you just walked right down to the river and started fishing."

Pacific Gas & Electric had already built Almanor, and the hydro era had begun by the time Larry started fishing. "The word was that the Feather had been a world class fishery and the dam had killed it…it had already gone downhill by the time I fished it…I guess the dam cut off the spawning grounds; it must have gone pretty damn fast."

But the river—though a shadow of its former self—was far from dead. In 1926, two years before Larry first fished the Feather, an enormous rainbow trout was caught there. At 21 pounds, 3 ounces that fish set a new State record which stands to this day.

Fishing was only possible when peak power demand was down, and the flows out of Almanor dropped. When word came up to the gold mine where Larry was working that the flows were dropping Larry and his co-workers would drop their tools and go.

"When the water was low, Uncle Oscar was looking for 12-14 inch trout, all rainbows, and he got 'em every time. The limit was 20 trout, and we always just caught enough to satisfy our needs. The rest we'd just shake off. We never needed a limit; we'd go down in the evening and fish till it was dark, and we always had enough fish for food. We didn't have ice up there, so you didn't want to keep more than you could eat."

Special FEATURE

Larry, a founding member of CalTrout, hasn't lost the "fire in the belly" either. He's busy opposing a local dam project on the Yuba River: Parks Bar Dam just above where Highway 20 crosses near Timbuktu bend.

"I've hunted and I've trapped and I've fished, and I've had a wonderful time. I've been really lucky."

Water to a Dusty Stream

NEGOTIATIONS BEGIN TO RE-WATER SANTA ANA RIVER

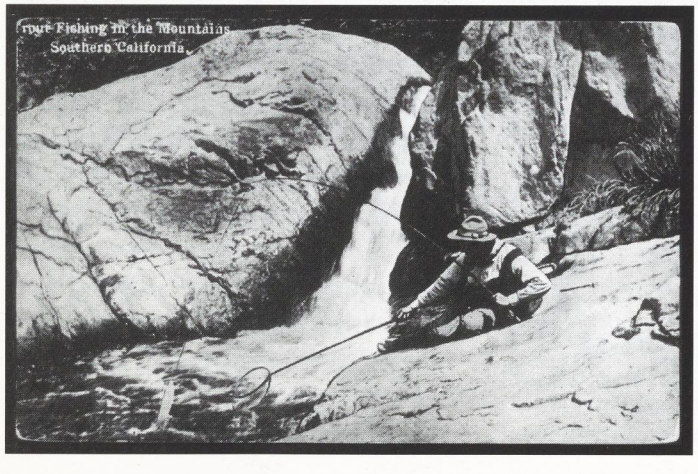
"There are many streams teeming with trout in Southern California. Out of Pasadena, San Diego, Pomona, Ontario, and especially up the San Bernardino range in the headwaters of the Santa Ana, fine fishing streams are to be found. Here trout find congenial habitat, plenty of cold, pure, running water and almost ideal spawning grounds." George W. James. *Traveler's Hand Book to Southern California.* 1904.

That all changed in 1906, the year the Santa Ana was dammed and diverted for hydro-power. Ever since, the headwaters of the Santa Ana River have been bone-dry. This has been condoned by the Federal Energy Regulatory Commission (FERC) who has twice issued 50-year hydro-power licenses to the Southern California Edison Company (SCE).

Since 1986, FERC has been ordered by Congress to balance hydro-power interests with environmental concerns, so old license terms that allowed for dry streambeds will have to be revisited. This is happening right now for tributaries of the Santa Ana River, nestled high in the mountains of the San Bernardino National Forest.

Dry streambeds make for poor trout streams. So in 1992 CalTrout began applying pressure to bring FERC and SCE to the bargaining table, a place they preferred to avoid.

In order to get them to the table, CalTrout pointed out serious flaws within SCE's pre-licensing environmental analysis. For example: SCE's Santa Ana River instream flow study and its related stream temperature investigation



were first rate analytical documents, but unfortunately were conducted on a purely theoretical basis—without any water in the river. Kudos to their theoreticians, but we needed to have a better sense of what sort of a trout fishery might exist under a new license.

After casting more than a shadow of doubt on the details of SCE's application for a new 50 year hydro-power license, we set out to build a powerful coalition of resource agencies and environmentalists determined to work towards recovered streams. This united front played a key role in bringing FERC and SCE to the table. Friends of the River, The Audubon Society, The Forest Service, DFG, the Fish & Wildlife Service, State and Regional

HYDRO-POWE

Water Boards, the City of Redlands, and dozens of local water districts found themselves around the table striving for a positive outcome to the current re-licensing effort.

Last summer FERC called all the interested parties together hoping to avoid an appearance in court. Attorney Richard Roos-Collins, and CalTrout exec Jim Edmondson, convinced the parties that a negotiated settlement was not only possible, but would certainly be more favorable than a FERC decision made 3,000 miles away. "I can guarantee all parties present that no one would like that distant decision," said Edmondson.

At first, SCE and their beneficiaries, the local water

agencies, dug in their heels, and the meetings appeared to be heading nowhere fast. However, last February, CalTrout brought an alternative to the table: *pick a stream reach, and try to negotiate a settlement where the controversies are smallest.* The parties agreed.

By late March discussion over re-watering approximately five miles of the Upper Santa Ana river began in earnest. CalTrout is advocating a conservative and adaptive management approach for settlement. We hope to persuade the parties to take three key steps: 1) identify in measurable terms the fish population they want to restore, 2) release water in a carefully monitored program, and 3) if the fishery responds as anticipated—done deal. If not, add more water. This process will minimize SCE's risk in re-watering streams, while providing water delivery and restored ecosystems, to boot.

If these negotiations bear fruit, the parties will turn their attention towards seeking agreement for two other Santa Ana tributaries, Lytle and Mill Creeks, which both have similar hydro projects on them. All in all, this re-licensing project encompasses about 20 miles of trout streams. In Southern California, that's a lavish amount.

River for Sale?

DFG-NMFS SELL SHORT ON EEL RIVER

In a joint filing, representatives of Pacific Gas & Electric Company (PG&E), the California Department of Fish & Game (DFG), and the National Marine Fisheries Service (NMFS) agreed on a flawed proposal for Eel River flows below PG&E's controversial Potter Valley Project diversion.

However, after a last minute review of all available information, the United States Fish & Wildlife Service (USFWS), rejected the proposal. This astounding about-face had CalTrout, Humboldt County representatives, and Round Valley Tribe representatives elated.

"Whatever the 'biologists' at the DFG and NMFS may think, there is no way on God's Green Earth to justify five cubic feet per second flows on the mighty Eel River...we applaud the United States Fish & Wildlife Service for recognizing that fact," said CalTrout's Hydro Reform Coordinator Michael Bowen.

In a letter, the USFWS , expressed strong support for the aspects of the proposal introduced by CalTrout, but they expressed stronger reservations about the details and implementation pitfalls of the proposal. CalTrout shares these concerns, and has expressed them frequently. The USFWS apparently recognizes the impossibility of effectively implementing PG&E's proposal, as well as the importance of not abandoning over 30 kilometers of steelhead rearing habitat below the dam.

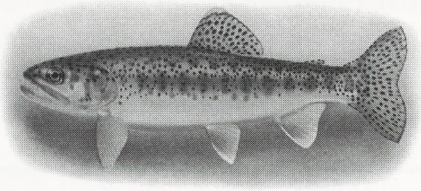
Cynthia Barry, Acting Assistant Regional Director of the USFWS wrote "...Specifically, the Service approves of the concept of proposing a relationship between flow releases and natural accretion events in the Eel River watershed...If properly implemented...(this) could dramatically improve the viability of the salmon and steelhead populations in the Eel River." She then lists a number of reasons why the USFWS cannot support the proposal.

In exchange for supporting this proposal, PG&E offered the DFG $60,000 per year for programs to mitigate the project impact on fishery resources. Regretably, the DFG accepted.

"$60,000 is pretty cheap for a river, but we're learning not to be surprised by anything Region III of the DFG does anymore," said Bowen, continuing, "...kudos to the Fish & Wildlife Service for taking their trustee responsibility to the resource and to the Tribe seriously."

(California Gold: continued from cover)

The Commission responded enthusiastically, directing the Department of Fish & Game (DFG) to establish a Wild Trout Program for the management of California's wild trout resources. What followed is the stuff of tall tales, and the Wild Trout Program is now one of the DFG's most spectacularly popular and successful programs.



Now, more than a quarter century later, California's *native* trout are ready for a new level of appreciation and protection. This May CalTrout will appear before the Commission to ask for the creation of a new program:

WILD TROUT *Program*

The Wild Trout Heritage Program. This program would be specifically designed to provide another layer of protection and enhancement for California's native trout species.

Once the Commission has heard our proposal, they may direct the Department to investigate the potential of such a program. If the Department concurs, the Department and CalTrout could then work together to seek State legislation for creating the program. Once passed, the final component will be to work with the Federal land management agencies and Federal legislators to prepare a new Memorandum of Understanding addressing the protection of these fish on federal lands.

Boasting ten different species and various strains of native trout, California's assemblage of native trout species is unprecedented in the world. Most anglers know that California's trout species have been disseminated around the globe, as far away as South Africa and Patagonia, but many anglers don't know that a tremendous diversity can be found in their own backyard

The Heritage Trout Waters Program, if accepted, is intended to fill that gap. If adopted, the program will help to educate California's anglers about these unique species, and encourage anglers to diversify their angling experience. As public appreciation of these diverse species grows, support and funding for additional programs to restore ailing fish stocks may follow.

California's Unique Trout Species

Lahontan cutthroat trout
Onchorhynchus clarki henshawi
Piute cutthroat trout
Onchorhynchus c. seleniris
Coastal cutthroat trout
Onchorhynchus c. clarki
Coastal rainbow trout
Onchorhynchus mykiss irideus
Eagle Lake rainbow trout
Onchorhynchus m. aquilarum
McCloud River redband trout
*Onchorhynchus m. subspecies**
Goose Lake redband trout
*Onchorhynchus m. subspecies**
Warner Lakes redband trout
*Onchorhynchus m. subspecies**
Kern River rainbow trout
Onchorhynchus m. gilberti
Little Kern golden trout
Onchorhynchus m. whitei
Volcano Creek golden trout
Onchorhynchus m. aquabonita
Dolly Varden trout (EXTINCT)
Salvelinus confluentus

*These subspecies are awaiting "scientific description" by fish taxonomists and geneticists and are part of a complex of redband trout that have been isolated from coastal rainbow trout in interior drainages.

Already, one fish has been lost, although it is a char and not a trout species. Now is the time to ensure added protection of the other species through the Heritage Program.

Proposed Heritage Policy for the Fish & Game Commission

- Heritage waters shall be open to public angling and designated to promote recognition of the beauty, diversity and special values of California's native trout species.
- Only waters with the purest strains of native trout within their original range qualify for designation.
- Angling regulations shall be adopted and maintained which assure that angling does not significantly impact the abundance and size structure of a stream or lake's native trout population.
- All necessary actions, consistent with state law, shall be taken by the Department of Fish & Game to prevent adverse impacts by land or water development projects on designated Heritage Trout waters.
- A new Memorandum of Understanding with the State and Federal land management agencies will be developed to maintain or improve these watersheds in pristine condition. Pristine condition means the natural condition of an area when human induced influences are removed. These influences include timber harvest, road construction, mining, livestock grazing, and heavy recreational use.

Increased public awareness of these areas will increase their value. Managed enjoyment of Heritage Trout Waters can increase greatly the diversity of local economies.

UPDATES *and* ACKNOWLEDGEMENTS

TMDL Update

The Total Maximum Daily Load (TMDL) process hasn't been easy on Bob Klamt. As the Senior Land and Water Use Analyst for the North Coast Regional Water Quality Control Board (RWQCB), Bob faces the daunting challenge of bringing our North Coast rivers up to snuff on new temperature, turbidity, and other water quality issues. Naturally, this new duty hasn't been met with commensurate increases in funding, but Bob's keeping a stiff upper lip.

"The TMDL process is a scary, ominous workload for my agency...on the other hand, it's a good mechanism to get the changes we need to recover our North Coast rivers," said Klamt.

Bob provided us with a number of corrections to our previous article which we gladly reprint here:

1) The TMDL process does not set "standards" in the legal sense, for North Coast rivers. It sets targets which call for the implementation of various erosion and sediment control measures believed capable of achieving the desired targets.

2) The time schedule published in the last issue was outdated. Most importantly, the final deadline for the last of the North Coast rivers is 2007. If you are interested, contact CalTrout for an updated list.

The RWQCB will work closely with the Environmental Protection Agency to meet the deadline, but more importantly, the RWQCB hopes to work closely with groups like CalTrout to meet the deadline.

According to Klamt, "TMDL represents a tremendous opportunity to initiate real watershed planning...in order to make it work, we need any information groups like CalTrout can provide in order to help us stay ahead of the curve on this process."

California Trout would like to thank the following individuals, clubs and businesses that made membership contributions of $250 or more and joined our new Wild Trout Circle, or Golden Trout Circle since the publication of the last issue of the Log. These folks are providing the extra bucks we need to get our jobs done.

Golden Trout Circle ($1,000 or more)

James H. Greene, Jr
Maurice E. Holloway
Mark Ohanian
George and Faye Saul

Clubs

The Conejo Valley Fly Fishers

Wild Trout Circle ($250 to $999)

William J. Argo, M.D.
William L Berry, Jr.
Frank M. Brown
Steve Castleberry and Nieret Mizushima
David and Susan Coulter
Jim De Bar
Geza Demeter
David A. Dennis
Doug Durham
Richard L. Fischer
Mrs. Edmond S. Gillette, Jr.
William S. Greenough
Frank Hainley
John B. Healy
Donald F. Imwalle
Dwight L. Johnson
Albert W. Kelley
Bill Kennedy
Mike and MiYoung Kleine
Byron W. Leydecker
Randle E. Lindberg
Fred Mathis
Chuck Newmyer
John Peckham
Andrew S. Pomerantz
James S. Taylor
Tomas C. Tisone
David and Pat Travis
John C. Wallace
Matt Watson
Peter Wells
Robert S. Young

Businesses and Clubs

Flycasters, Inc.
Industrial Tenant Improvement, Inc.
Lyon Ventures, Inc.

Foundations

The Drummond Family Fund of the Oregon Community Foundation
The Mennen Environmental Foundation

Correction...

The Donald Barrie Memorial Fund was spelled incorrectly in the last issue of the Streamkeepers Log. We apologize for the error.

We need your help!

Have you ever heard of Earth Share of California? It is the work-place giving federation for California's environmental organizations and it represents California Trout. Like the United Way, Earth Share allows California Trout to raise money in the workplace by running campaigns in companies. Earth Share has also been one of the best ways that CalTrout raises money—it does not take up too much staff time and it allows us access to thousands of California citizens that we would have no other way of reaching.

If you think that the company you work for is a good candidate for an Earth Share of California workplace giving campaign please call our Development Director, Traci McCollister at 415/392-8887. She would be happy to discuss it with you. CalTrout receives a special bonus for every new campaign we start—this could run into some serious new money. This is an excellent opportunity for members to help the organization raise much-needed money!

❑ $30 Regular Member ❑ $50 Contributor
❑ $100 Donor ❑ $250 Wild Trout Circle

Membership dues are on a calendar year basis, just like your fishing license, but are fully tax deductible. All members receive subscription to CalTrout publications, free emblems, and full voting rights.

Name _____

Address _____

City _____

State _____ Zip _____

California Trout
870 Market Street, Suite 859
San Francisco, California 94102-2903

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Name _____

Address _____

City _____

State _____ Zip _____

California Trout
870 Market Street, Suite 859
San Francisco, California 94102-2903

You love to fish for trout. You love the streams, rivers and lakes where trout live. The relationship is direct: when trout are protected, rivers are protected; when rivers are protected, watersheds are protected. The dream is to restore trout and steelhead resources to what they were in early California.
Conservation makes it possible.

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CALIFORNIA COASTAL COMMISSION
SOUTH CENTRAL COAST AREA
89 SOUTH CALIFORNIA STREET, SUITE 200
VENTURA, CA 93001
(805) 641-0142

December 29, 1997

IMPORTANT PUBLIC HEARING NOTICE

APPEAL

PERMIT NUMBER: **A-4-STB-97-131**

APPLICANT(S): **Caltrans**

APPELLANT(S): **Mr. Geoffrey Latham**

DECISION BEING APPEALED:

Realign a portion of Highway 150 and bebuild bridge 51-141 and move and replace bridge 51-140, 60 ft. south.

PROJECT LOCATION:

One To Two Miles Inland From The Intersection Of Highway 150 Along The Santa Barbara/Ventura Co. Border In The Carpinteria Area, Santa Barbara County (APN(s) 001-200-23, 001-440-04, 1000-450-02, 1000-450-05)

HEARING DATE AND LOCATION:

DATE: **Monday, January 12, 1998**

TIME: **Meeting begins at 10:00 AM** ITEM NO: **M22a&b**

PLACE: Embassy Suites - San Luis Obispo
333 Madonna Road, San Luis Obispo, CA 93405
(805) 549-0800

HEARING PROCEDURES:

People wishing to testify on this matter may appear at the hearing or may present their concerns by letter to the Commission on or before the hearing date. Copies of all correspondence will be provided to the Commission if received a minimum of three working days prior to the public hearing. Written comments may be of any length; oral testimony may be limited to 5 minutes or less for each speaker, depending on the number wishing to be heard.

Section 30625(b) of the Coastal Act requires the Commission to hear an appeal unless the Commission determines that no substantial issue is raised by the appeal. In its consideration of whether the appeal raises a substantial issue, the Commission may decide to take testimony from the public. In that case, proponents and opponents will have three minutes per side to address whether the appeal raises a substantial issue. If the Commission finds that a substantial issue is raised the Commission will proceed to a de novo public hearing on the merits of the project. If the Commission finds that no substantial issue is raised, the local government's action on the coastal development permit is final.

No one can predict how quickly the Commission will complete agenda items or how many will be postponed to a later date. The Commission begins each session at the time listed and considers each item in order, except in extraordinary circumstances. Staff at the appropriate Commission office can give you more information prior to the hearing date.

Questions regarding the report or the hearing should be directed to Mark Capelli, Coastal Program Analyst, at the South Central Coast Area office.

"STATE OF CALIFORNIA—THE RESOURCES AGENCY PETE WILSON, Governor

CALIFORNIA COASTAL COMMISSION
SOUTH CENTRAL COAST AREA
89 SOUTH CALIFORNIA ST., SUITE 200
VENTURA, CA 93001
(805) 641-0142

DENIAL OF RECONSIDERATION

Date: February 13, 1998

Permit Application No. A-4-96-318R
Permit Application No. A-4-97-131R

~~This is to advise you that on~~ January 12, 1998, the California Coastal Commission denied the development proposal described in the attached material. The denial pertains only to this proposal and does not affect other proposals that may have been made or may subsequently be made for development of the subject parcel. Pursuant to 14 Cal. Admin. Code 13109, you may not reapply for a coastal development permit for substantially the same development for a period of six months from the date of the Commission's decision.

Peter M. Douglas
Executive Director

By: MERLE E. BETZ, JR.
Coastal Program Analyst

Enclosure

A9:8253Apg8/sm

From the desk of Ed Henke
HISTORICAL RESEARCH

5/20/98

DR. BEHNKE —

THANKS FOR YOUR RECENT (ENJOYED) NOTE and ENCLOSURE. ENCLOSED (RECENT) IS MINE ON CALIFORNIA'S INCOMPARABLE "CDFG" HEADED up BY Gov. WILSON. My BIASES don't MEAN IS NEAR AS MUCH AS ZONES. I told MC EVAN THAT I'M BE RELENTLESS IN MY EFFORTS.

BEST REGARDS — Ed Henke

Ed Henke
Historical Research
769 Lisa Lane • Ashland, Oregon 97520 • 541-482-9578

May 20, 1998

Dr. William T. Hogarth, Ph.D.
Regional Administrator
U.S. Department of Commerce
NOAA/NMFS/SWR
501 W Ocean Blvd., Suite 4200
Long Beach CA 90802-4213

RE: AGGRESSIVE PURSUIT OF "**APPROPRIATIONS**" FOR RINCON CREEK CULVERT MODIFICATION TO PROVIDE FOR A VIABLE ANADROMOUS FISH PASSAGE/CONVEYANCE SYSTEM

DECLARE RINCON CREEK, ITS RIPARIAN HABITAT AND ITS ENTIRE WATERSHED AREA LOCATED WITHIN THE LOS PADRES NATIONAL FOREST AS "**CRITICAL HABITAT**"

ATTN: Eric Schott

Dear Eric:

Thank you for the courtesies extended during our recent telecon regarding my correspondence to Dr. Hogarth involving a copy of a draft presentation sent to him titled: "A Case for the Removal of Matilija Dam ..." He, in turn, advised that future communication should be through Eric Schott, so here I am again.

During our conversation you advised that input to you relative to documentation of recent fish sitings (Steelhead) would be of valuable importance to you. Under separate cover, I'll be advising you of such information regarding the Ventura River. As for this communication, it involves a long lingering unresolved issue and legal obligation by the State of California to provide for a viable and easily accessible conveyance system for anadromous/migratory salmonids (Steelhead) so that they can successfully migrate/emigrate in/out of Rincon Creek.

In a recent communication with Dennis McEwan, California Department of Fish and Game, he indicated that the **fish passage** project is **dead** for Rincon Creek because the **California Coastal Commission** denied the Cal-Trans bridge alignment project for Rincon Creek. The reason given for the **fish passage** project **being dead** was that the funds Cal-Trans was to match with the California Department of Fish and Game funds to construct the "**fish-way**" would no longer be available as a result of the denial by the Coastal Commission. My colleagues and I see it clearly as two separate and distinct issues: (1) Cal-Trans seeking a permit for bridge construction and (2) the State's legal obligation to build a viable **fish passage** facility. Further, he indicated that he was trying hard to divert the Rincon Creek **fish passage** facility funds to the **Robles**

Diversion Dam-Canal project on the Ventura River, where even more complex conditions have prevailed for some 40 years now! This project also appeared **negative** to him due to their (CDFG's) funding deadlines. From a legal standpoint, Cal-Trans and the Casitas Municipal Water District should be 100% responsible for building such "**fish-ways**" and "**fish-screens**." It is obvious to many that the State of California and its hierarchy well above Mr. McEwan's level are not in sync with the intent or spirit of the Federal "Endangered Species Act" and for the very survival of anadromous salmonids in general... There is absolutely no sense of urgency by top State government officials to comply with the Federal "Endangered Species Act" mandate.

You will note by the enclosed copies of correspondence that a cost of $550,000 was estimated by Cal-Trans to build the "**fish-way**," with a commitment to provide $200,000... The California Department of Fish and Game budgeted for $350,000. A professional in the field of aquatic resources who has personally examined the problem says successful modification can be accomplished for much less money.

Also, you will note within the enclosed correspondence that Steelhead/native resident trout (Oncorhynchus mykiss) were determined to be extirpated from Rincon Creek via the results of a stream analysis survey made in 1994. There is contrary evidence to this statement and another that these fish were extirpated possibly as early as the 1960s. We all know that catastrophic natural events, such as fires, earthquakes, etc., have occurred for thousands of years, and the most resilient Southern Steelhead have survived it all. They are wanderers, meanderers, and recolonizers, and while maybe not to the same degree or extent, their counterparts elsewhere do the same... Historically, that's how anadromous salmonids extended their range. They also may survive at sea for who knows how many years as a maximum. Extirpation of the natural migrations of Steelhead into Rincon Creek was not over as early as the 1960s or as the 1994 survey results had indicated, but the ultimate survivors just temporarily changed their residence... Documentation indicates their ongoing presence.

ON NOVEMBER 4, 1997, I VISITED WITH DR. WALTER BARROWS, PH.D., AT HIS RANCH ON RINCON CREEK. HE TOOK ME DOWN TO THE CREEK IN THE EVENING AND POINTED OUT 5 TO 6 SMALL JUVENILE STEELHEAD APPROXIMATELY 6 INCHES LONG RUSHING AROUND IN THE POOL DIRECTLY BELOW THE LAST ROAD CROSSING NEAR HIS HOME. HE ALSO ADVISED THAT OVER THE PAST TWO YEARS HE HAD OBSERVED NUMEROUS FISH OF THE SAME APPROXIMATE SIZE UPRIVER ABOVE THE OLD ARCO QUARRY MINING OPERATION, 1 TO 2 MILES UPSTREAM FROM HIS RANCH.

It appears, through this additional evaluation, that irrespective of the inadequacy of the pipe below the Highway 101 bridge to allow for normal fish passage, the indomitable determination of these fish has allowed more than one to make it through such egregious conditions in order to perpetuate the species.

Additionally, and to add to the equation, no one has yet to relate to another manmade, long enduring, major obstacle that has truly inhibited anadromous/migratory salmonids from reaching the largest portion and limit of their historical natural spawning and rearing habitat in Rincon Creek, all of which is located in the U.S. Los Padres National Forest, **Public Trust Lands**: The Arco Corporation's mining and quarry operation, which existed over an approximate seven-year period, was located directly in the bedrock of Rincon Creek, as well as on both sides.

The following is an abbreviated accounting of information that I obtained regarding the quarry operation and some of its most obvious results and fallout: Predicatable deleterious effects to the creek's aquatic resources' biodiversity and general egregious conditions...

> The Arco Corporation evidently initiated a staked claim process through the Federal government/U.S. Forest Service, which successfully provided them a **permit** to mine an unlimited amount of rock directly from Rincon Creek's live riverbed channel as well as on both sides (the creek's riparian habitat), all of which is located within the boundaries of the Los Padres National Forest— **Public Trust Assets** and **Public Trust Lands.** The vehicle that allowed them to acquire such a right/claim was through an antiquated Federal Mining Claim Act of 1870... In essence, the Act projected approximately 80 years in advance that Arco would still have such a right on **Public Lands** that had yet to be created ... and apparently, without much scrutiny. And, at what level of compensation to the Federal Government?
>
> The quarry was mined for the benefit of the Arco Corporation to build an offshore oil island and a special pier. This mining operation started in the 1950s and was completed approximately seven years later in the 1960s.
>
> A short distance below the quarry site and close to Rincon Creek was Dr. Walter Barrows' residence. Directly across the creek from his residence, the contractors for the mining operation had set up a weigh/scale house for the big rigs laden with large rock to check through. The carrying beds of these large rigs were made from old railroad cars cut in half. This was a 24-hour around the clock operation that endured over the approximate seven-year period, extracting rocks directly out of the creek's bedrock/channel and on both sides/riparian areas. Large dynamite blasts were common and all "**spoils/waste**" ended up piled on both sides as well as being physically dumped some 200-300 feet above the original bedrock. Also in the process, they built "**revetment debris basins**" in the creek's channel some 10-12 feet high. Some of the quarry's "**waste**" was used in the widening of Highway 101,

so Cal-Trans/State of California was also involved. This whole quarry operation was located approximately 3 miles from the ocean.

Dr. Walter Barrows purchased and acquired his ranch property in June 1959, giving him 11.23 acres of land along Rincon Creek, a portion of which abutted U.S. Forest Service lands, the boundary of which was 190 feet from the new family dwelling. Following a 1963 flooding, he had $179,000 of out-of-pocket expenses to build revetment on Rincon Creek next to his property to protect the loss of additional riparian habitat and for flood protection. The 1963 waters had raged 10 feet over the top of his road crossing. Normally the creek at this point was 20 feet wide and 2-3 feet deep. The waters were now spread out over a 100-foot area, with flows of water now on both sides of his new house. When the large volume of water started moving through the upriver denuded section of the creek bed, all sizes and shapes of aggregate/rock/debris came tumbling down toward his property. The bed load was too great to flush, with a boulder six feet in diameter being dislodged upstream and lodging directly in front of the Barrows' house. Through all of this, the Barrows received no help or relief from either Santa Barbara County or Ventura County, as both denied any responsibility for what had or had not transpired as a result of this whole scenario, either upstream or downstream.

DURING THIS ENTIRE PERIOD, HIS CHILDREN WERE CATCHING SMALL JUVENILE STEELHEAD OUT OF RINCON CREEK ALONG THEIR PROPERTY LINE UP TO 12 INCHES, ALL OF WHICH WERE RELEASED. THIS WAS, OF COURSE, BELOW THE MINING OPERATION.

In 1963, the U.S. Army Corps of Engineers announced they were going to channelize Rincon Creek just below the quarry to Highway 150, and ultimately channelized all the way to the ocean, some 3 miles. In the process, they cut down sycamores, willows, alders, and maples, all of which were native species, with some 300-400 years old… and other.

Nowhere during the process of obtaining this information did I detect any initial/up-front involvement by biologists or enforcement personnel from the U.S. Fish and Wildlife Service, U.S. Forest Service, or the California Department of Fish and Game. Obviously, these were/are manmade barriers/impediments (possessing other destructive features) to anadromous fish migration/emigration in/out of Rincon Creek.

It is thereby respectfully requested that the National Marine Fisheries Service, in conjunction with the U.S. Forest Service and the California Department of Fish and Game (and others?), reach a consensus agreement that Rincon Creek, its riparian

habitat, and the entire Los Padres National Forest watershed area serving Rincon Creek be declared as **CRITICAL HABITAT** for the Southern Steelhead under the Federal "Endangered Species Act." Also, it is respectfully requested that the same decision making bodies, in conjunction with other appropriate governmental agencies, immediately appropriate the necessary funds to construct a long overdue "**fish-way**" in the culvert below the Highway 101 bridge on Rincon Creek. We have assumed that the contractor ultimately selected for such construction will be chosen through the free enterprise competitive bidding process.

I can arrange for access to property owners along Rincon Creek by National Marine Fishery Service personnel for interviews and who will also be in support of such recommended actions. We hope that a **sense of urgency** will prevail and the whole process will proceed accordingly.

Thank you very much.

Best personal regards.

Sincerely,

Ed Henke

cc: Geoffrey Latham, Esq. (Rincon Creek area resident)

[In reprint Sides]

CITY OF HOPE MEDICAL CENTER
DUARTE, CALIFORNIA

DEPARTMENT OF BIOLOGY

December 31, 1968

Dr. Robert J. Behnke
Colorado Cooperative Fishery Unit
102 Coop. Units Building
COLORADO STATE UNIVERSITY
Fort Collins, Colorado 80521

Dear Dr. Behnke:

It was a pleasure to have had the chance of meeting you in Dallas. Enclosed please find reprints of some of our papers on fish which may be of interest to you.

Sincerely yours,

Susumu Ohno

Dr. Susumu Ohno, Chairman
Department of Biology
City of Hope Medical Center

SO:sb
Encl.