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Whirling Disease in California: A Review of Its History, Distribution, and Impacts, 1965–1997

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Abstract.—*Myxobolus cerebralis*, the causative agent of whirling disease, has become widely established in wild California salmonid populations since its initial discovery in Monterey County in 1965. Most significant is the occurrence of the parasite in the "blue ribbon" trout waters of the Owens Valley basin of the eastern Sierra. From the Lahontan basin on the north to the Owens Valley basin 320 km to the south, the parasite has become well established. In spite of the presence of the parasite, streams of the eastern Sierra are considered by many to support high quality trout populations, attracting thousands of anglers annually to the region. Empirical observations suggest that fish populations are healthy in the Owens Valley drainage and in the *M. cerebralis*-positive waters of the Lahontan and Pacific drainages. These observations are supported by population data comparing populations of rainbow trout *Oncorhynchus mykiss* and brown trout *Salmo trutta* on Sagehen Creek and the lower Truckee River in the Lahontan basin, and rainbow trout populations in *M. cerebralis*-positive and -negative sections of the Carmel River on the central California coast near Monterey. The chronological appearance and distribution of *M. cerebralis* strongly implicates dispersal of live or processed state and commercially produced fish as a major factor in the spread of the parasite in California. Infected anadromous stocks have not appeared to spread detectable levels of *M. cerebralis* into numerous coastal waters and waters entering directly into San Francisco Bay. A severe epizootic of *M. cerebralis* at the Mt. Whitney State Fish Hatchery in the spring of 1995 confirmed the virulent potential of *M. cerebralis* in California. Spores of *M. cerebralis* can no longer be detected in wild populations at three locations since elimination of the source of infection in those waters.

The causative agent of whirling disease (WD), *Myxobolus cerebralis,* has been known to infect both domestic and wild salmonid fish populations in California since 1965. Confirmation of a hatchery epizootic that began in June 1965 at a small private trout farm on Garrapata Creek near Monterey was made in January 1966 (Horsch 1987). Between 1965 and 1984, five commercial growers and one state fish hatchery had fish diagnosed with clinical WD. In each case prior to 1984, infected stocks were destroyed and cleanup efforts were undertaken by the California Department of Fish and Game (CFG). The estimated number of fish destroyed by CFG directives during 1965 through 1984 include 660,000 kg of catchable and broodstock fish and approximately 2,300,000 fingerlings and subcatchable fish.

Sampling efforts to determine the geographical range of *M. cerebralis* intensified in California following its discovery at two commercial trout operations in central California in 1982 and 1983 and in CFG stocks at Mt. Whitney State Fish Hatchery (MWH) in 1984. Before then, *M. cerebralis* was thought to be limited to coastal waters of Monterey Bay and the Lahontan basin drainages of the eastern Sierra entering Nevada. Recognition of a more widespread distribution led to an increased sampling effort that resulted in sample collections from wide-ranging venues by both CFG Fish Health Laboratory personnel and regional and staff fishery biologists.

This paper reviews the history of *M. cerebralis* in California, discusses a scenario strongly implicating unwitting state and commercial dispersments of subclinically infected stocks as a major factor in its distribution, and presents arguments suggesting that California's climate and topography may be among factors contributing to the minimal impacts observed on wild California salmonid populations. These observations may explain why major impacts are reported in some regions (Montana and Colorado) but not in California and other western and eastern states.

Methods

The numbers of fish available for testing varied considerably throughout the extended sampling period. Factors that influenced the number of fish sampled included water conditions at the time of collection, sampling protocols of studies not related to fish health, and concerns for taking large numbers of already depleted wild, native fish. Gen-

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erally, sample sizes were between 30 and 40 fish that were pooled into five or fewer fish per sample for testing. Many sites were sampled on a multiple-year basis between 1985 and 1997 to maintain current knowledge of previously identified positive sites. Samples were normally frozen prior to preparation and processed by the plankton centrifuge method described in the "Fish Health Blue Book" (Thoesen 1994).

Confirmation was normally made by histological identification of spores infecting cartilaginous tissues. In waters where spore counts were low or intermittent and where no clinical presentations were observed, identification was based on spore size and morphology characteristic of *M. cerebralis* recovered from cranial skeletal tissues. Electrofishing methods used to acquire population data reported by the Monterey Peninsula Water Management District (MPWMD) and CFG personnel are available from MPWMD and CFG administrative files.

Results and Discussion

Sampling of wild fish populations since 1984 revealed many new sites positive for *M. cerebralis* in California despite eradication and cleanup efforts. Distribution of subclinically infected state and commercial live fish prior to our identification, eradication, and cleanup efforts is the most likely cause of these new positive findings. Our early aggressive fish destruction and cleanup policies did not resolve the problem of recovering infected fish released over an unknown but perhaps extended period of time. The new discoveries and lack of recognition by CFG regional and staff fishery biologists and fish health laboratory personnel of impacts on rainbow trout *Oncorhynchus mykiss* (RT), brown trout *Salmo trutta* (BT), and golden trout *O. aguabonita* throughout the high-quality "blue ribbon" trout waters of the eastern Sierra led to a policy change that no longer required destruction of infected fish. Our present policy limits distributions of state and commercially infected stocks to known enzootic waters, or to terminal waters with no sustaining salmonid fish populations. Currently no state-produced fish are being planted in enzootic waters. Throughout the state, sampling efforts reveal little evidence of clinical disease or population declines. In waters where clinical presentations are found, clinical signs are generally limited to a variety of subtle cranial anomalies and vertebral column irregularities recognized only by fishery biologists who have been alerted about what to look for and by CFG Fish Health Laboratory staff. Rarely, significant skeletal anomalies are observed. In the 32 years since its discovery, blacktail or whirling symptoms have not been reported in any wild California salmonid populations. The subtle cranial depressions and vertebral column and lower jaw anomalies that are found are generally limited to fish from the Truckee, Carson, and Walker rivers in the Lahontan basin and in Aptos Creek, a small anadromous fish stream entering directly into Monterey Bay.

Cumulative negative natural and human-caused impacts on California fish populations including but not limited to fires, floods, drought, impoundments, and diversions allow few opportunities to accurately evaluate *M. cerebralis* impacts on wild populations. Nonquantitative empirical observations supported by population data presented below strongly suggest that no significant correlation exists between fish population numbers and *M. cerebralis* in California waters. In many *M. cerebralis*-positive waters cohabited by RT and BT, fish numbers and year-class composition appeared normal through multiple years of sampling.

Evidence of Parasite Decline

Since the closure of private aquacultural operations in the water supply, *M. cerebralis* has remained below detection levels for many years in two previously parasite-positive RT populations in California and in 1997 in a third RT population.

Wild RT populations in Garrapata Creek were found to be positive after the original discovery of *M. cerebralis* in domestic RT cultured in a private, earthen pond at this location in 1965. *Myxobolus cerebralis* has not been found in Garrapata Creek RT in recent years since the closure of that rearing operation. Multiple sampling efforts occurred between 1985 and 1997 to monitor the status of the original discovery site. Approximately 200 fish were sampled during the period. High stream gradients and lack of suitable tubificid habitat after closure of the facility may explain the decline of the parasite at this location.

At Coleman National Fish Hatchery (CFH) near Red Bluff, California, hatchery-reared RT were found to be positive for *M. cerebralis* in the mid-1980s. The parasite can no longer be found at CFH, either in hatchery stocks or in native salmonids collected from the hatchery water supply following closure of a *M. cerebralis*-positive, private processing facility in the upper drainage.

Myxobolus cerebralis was not detected in wild RT in the Carmel River in 1997. The decommissioning of an instream earthen RT rearing facility

TABLE 1.—Chronological sequence of identification of *M. cerebralis* from rainbow trout (RT) and brown trout (BT) in six major California drainage basins 1965–1995.

Date	Location[a]	Species	Status	Management action
1965	Central California coast (I), Garrapata Creek	Cultured RT	Epizootic	Destruction of stocks; facility closed
		Wild RT	Subclinical	None
1968	Lahontan Basin (II), Truckee River	Wild RT, BT	Occasional minor skeletal anomalies	None
1973	Central California coast (I), San Lorenzo River	Cultured RT	Epizootic	Destruction of stocks; facility closed
		Wild RT	Occasional minor skeletal anomalies	None
1982	West slope Sierra Nevada (II), Licking Fork Mokelumne River	Cultured RT	Epizootic	Destruction of stocks; facility closed
		Wild RT, BT	Subclinical	None
1983	West slope Sierra Nevada (III), Middle Fork Mokelumne River	Cultured RT	Subclinical	Destruction of stocks; restricted distribution[b]
		Wild RT, BT	Subclinical	None
1984	Eastern Sierra (IV), Owens River	Cultured RT, BT	Epizootic	Destruction of stocks; restricted distribution[c]
		Wild RT, BT	Subclinical	None
1985	Northeastern California (V), Tributaries of the Upper Sacramento River	Cultured RT	Subclinical	Restricted distributions[b]
		Wild RT, BT	Subclinical	None
1995	Southern California (VI), Santa Ana River	Wild RT, BT	Subclinical	None

[a] Roman numerals refer to drainage basins shown in Figure 1.
[b] Distributions of commercial stocks limited to enzootic waters.
[c] Distributions of state stocks limited to "terminal" nonsalmonid waters.

in the drainage in 1989 may explain the decline of the parasite at this location. The parasite could be detected during the drought years of the early 1990s, but it was not detected in 1997 following a return to flushing flows of normal water years after 1995.

These observations and similar examples in other California waters, where infections remain low grade or detectable only intermittently, support present CFG policy prohibiting distribution of known positive stocks of state-produced fish into known enzootic areas. The *M. cerebralis*-positive state hatchery at Mt. Whitney is operated exclusively as a broodstock station. Selected spent surviving broodstocks are planted into nonsalmonid "terminal waters" unsuitable for long-term survival and reproduction of salmonid fish. Two commercial aquaculturists are currently allowed distributions into historical markets in known enzootic waters due to livelihood considerations.

The apparent decline of *M. cerebralis* at Garrapata Creek, the Coleman National Fish Hatchery, and the Carmel River supports our present policy of restricted planting of *M. cerebralis*-positive stocks, to the greatest extent possible, into known enzootic waters.

In at least some waters, it appears that elimination of the source of infection results in parasite numbers falling to below detectable levels.

Virulence of the California Strain

Occurrence of normal looking, healthy salmonid populations in many California waters where *M. cerebralis* has been found has led some parasitologists to speculate on the existence of a less virulent California or West Coast strain infecting West Coast populations. Studies are underway to determine whether *M. cerebralis* in California is distinct from and perhaps less virulent than *M. cerebralis* found in other geographic areas of the United States. A recent experience at our *M. cerebralis*-positive Mt. Whitney State Fish Hatchery (MWH) in the eastern Sierra clearly demonstrates, strain variant or not, that the California form can cause considerable impact when afforded adequate environmental opportunity.

Broodstock selects normally hatched out and reared in *M. cerebralis*-free groundwater at the MWH's Black Rock Annex facility were incubated and reared in *M. cerebralis*-positive surface water at MWH in late spring of 1995. The results were devastating. By late summer, nearly 100% of the resulting fingerling fish were profoundly affected with blacktail, whirling behavior, and severe skel-

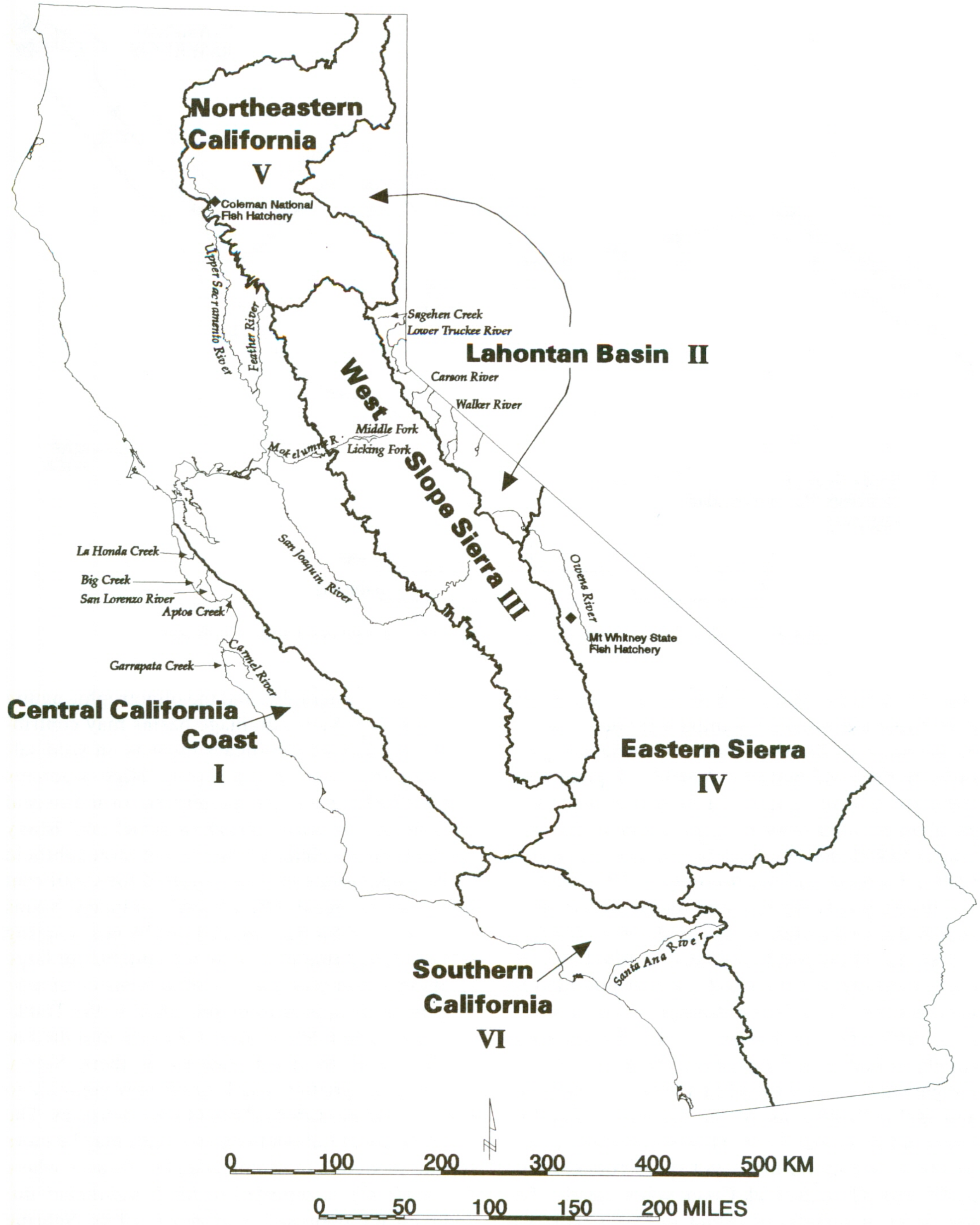

FIGURE 1.—Chronological sequence of identification of *M. cerebralis* in six major California drainage basins (I–VI) in 1965 though 1997, as indicated in Table 1.

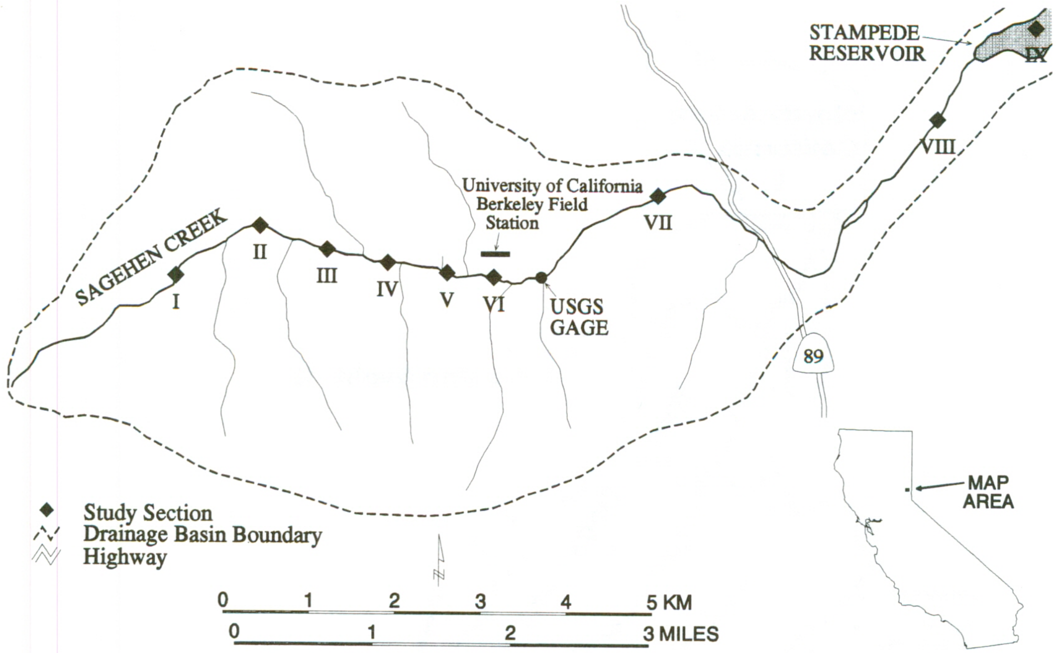

FIGURE 2.—Nine fish population study sites (I–IX) on Sagehen Creek, California.

etal deformities. Many fish were impaired to the extent that a normal swimming attitude could not be maintained, limiting most to disoriented positions on the pond bottoms. A wild fish population similarly affected could not have survived. This problem resulted from a unique water supply system at MWH that allowed an unusual buildup of tubificid worms and triactinomyxon life stages.

Settling ponds are required on the MWH water supply due to the high stream gradients of the eastern Sierra. These ponds had become filled over the years with organic mud and silt that provided an ideal habitat for a heavy tubificid worm population. Although the hatchery's Oak Creek water supply is known to be positive for *M. cerebralis,* the parasite was not found in a sample of both RT and BT collected above the hatchery after this event in September 1995. This observation is consistent with historic low-level spore counts found in RT and BT in the Oak Creek water supply. The low level of infectivity extant in Oak Creek was magnified many times in passage through heavy tubificid worm populations in the settling basins, which provided water to hatching sac fry and fingerlings. These conditions resulted in a massive WD epizootic and confirmed the virulent potential of *M. cerebralis* in California.

It can be speculated that combined conditions of climate, topography, and the oligotrophic nature of many west Sierra drainage basins may contribute to the lack of significant impacts on wild salmonid populations in California. High gradients and the flushing action of eastern Sierra and coastal streams due to heavy spring snowmelt and heavy winter rains preclude the buildup of large tubificid worm populations that are required for significant infections to occur. Oligotrophic drainage basins of the western Sierra characterized by heavy spring snowmelt and runoff also are not suitable for large tubificid worm populations. *Myxobolus cerebralis* detections do appear more prevalent in the Truckee, Carson, and Walker rivers flowing into the Lahontan basin from the eastern northern Sierra, where lower gradients and runoff may combine to result in greater tubificid population densities. The lower gradient Lahontan basin waters may be more typical of waters in Montana and Colorado, where *M. cerebralis* is reported to have significant impacts on RT populations (Vincent 1996; Nehring and Walker 1996).

Distribution

The current widespread distribution of *M. cerebralis* in California waters may be due in part to multiple unconfirmed factors, including migrating anadromous fish, fish-eating birds, and contami-

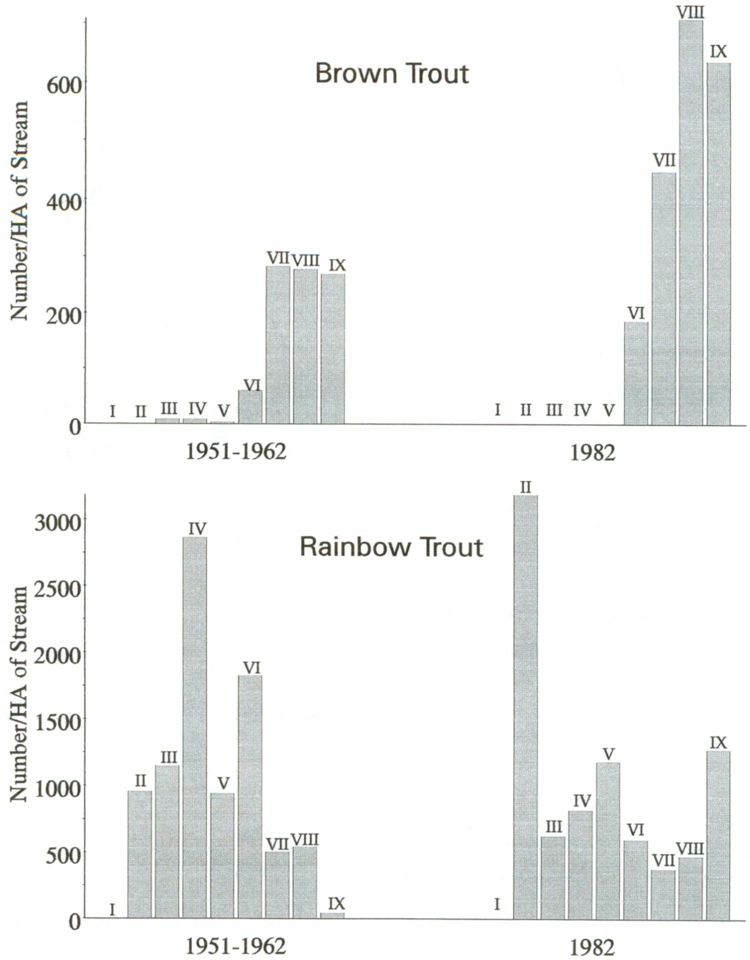

FIGURE 3.—Average lineal densities (number of fish/ha) of trout at nine sites on Sagehen Creek during 1951–1962 and in 1982. Roman numerals (I–IX) correspond to study sites in Figure 2.

nated boats, boots, and miscellaneous equipment used by anglers and others engaged in aquatic activities. However, the chronological appearance and presently known distribution pattern strongly implicate unwitting multiple transfers of subclinically infected live or processed stocks of state and commercially cultured product as the major factor in the distribution of *M. cerebralis* in California.

The following list outlines a possible *M. cerebralis* distribution scenario, from its discovery in Monterey and Nevada counties in the mid-1960s through 1997 (Table 1; Figure 1).

Central California coast, Monterey County, 1965.—A private grower reported whirling behavior in RT in an earthen production pond in June 1965. Whirling disease was confirmed in January 1966 and all fish were destroyed. Fish had reportedly been fed frozen, edible trout product from a Danish merchant vessel several months earlier. The infection was subsequently detected in native RT in waters below the hatchery.

Lahontan basin, Truckee, Carson, and Walker rivers.—*Myxobolus cerebralis* was discovered in wild RT and BT in 1968 in the Truckee River. It is suspected that the parasite's introduction into western Nevada occurred through importation of infected East Coast trout to Reno area restaurants.

Central California coast, Santa Cruz County, 1973.—A private grower reported whirling behavior in RT in earthen production ponds and *M. cerebralis* was confirmed. Straying RT infected with *M. cerebralis* or fish transfers between growers in Monterey and Santa Cruz counties probably resulted in the occurrence. All fish in the private

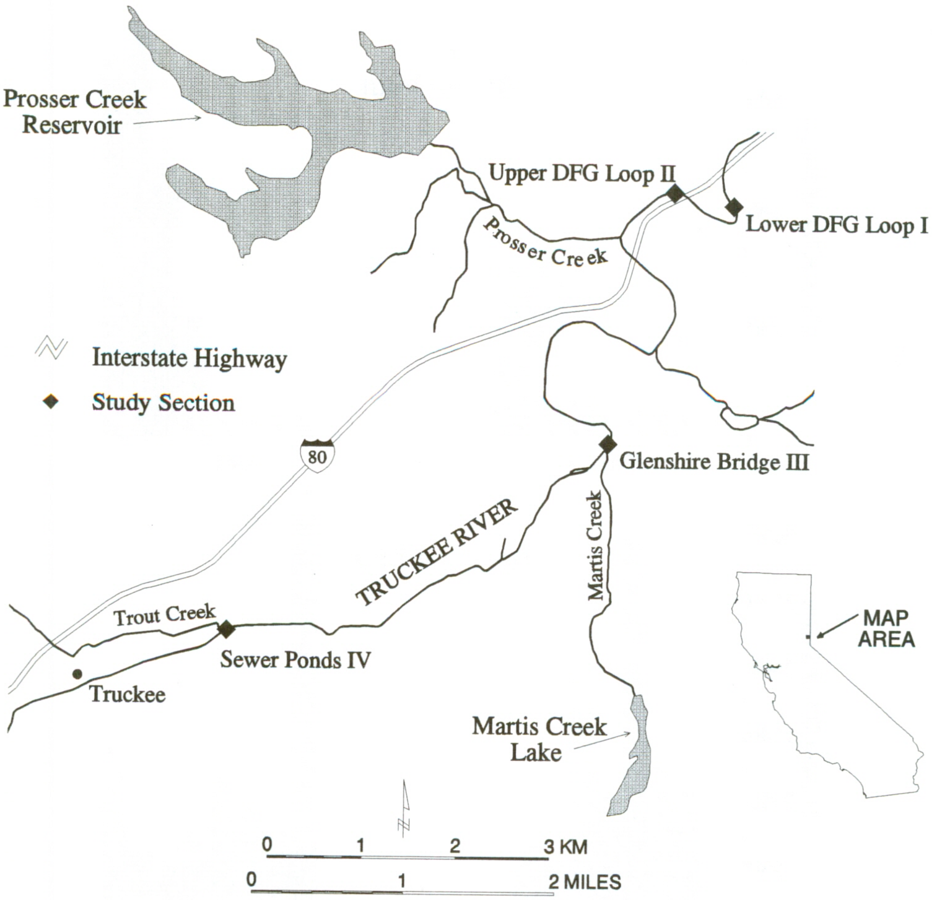

FIGURE 4.—Four fish population study sites (I–IV) on the Truckee River, California (DFG = California Department of Fish and Game).

hatchery were destroyed. Subsequently, *M. cerebralis* was found to be widespread in wild RT in the San Lorenzo River basin.

West slope Sierra Nevada, Mokelumne River, Calaveras County, 1982 and 1983.—Private growers reported whirling behavior in RT in two earthen production ponds. *Myxobolus cerebralis* was confirmed at both sites. All fish were destroyed. Fish transfers from a northern California producer subsequently found to be positive for *M. cerebralis* were reported by the Mokelumne River operators.

Eastern Sierra, Owens River basin 1984.—Whirling behavior was reported in RT and BT at the MWH. Whirling disease was confirmed and all production fish were destroyed. Multiple shipments from the northern California producer (subsequently found to be positive) had been made into Owens River basin waters over a multiyear period. Fish health examinations were conducted by CFG pathologists on all fish entering the Owens River basin for various fish pathogens and parasites. However, no *M. cerebralis* tests were conducted and no *M. cerebralis* signs were ever observed.

Northeastern California, streams tributary to the Upper Sacramento River, 1985.—Personal communication from George Du Four, hatchery owner, revealed multiple-fish transfers from his facility in Santa Cruz County to a "catch-out" pond–restaurant operation in northeastern California adjacent to a commercial fish operation. The commercial operation was found to have RT infected with *M. cerebralis* in 1985, but it is not known how long the infection might have been present.

Southern California, Santa Ana River, 1995.—*Myxobolus cerebralis* was discovered in wild RT in the upper Santa Ana River during routine sampling. This infection was most likely extant but undetected for many years. A local trout producer

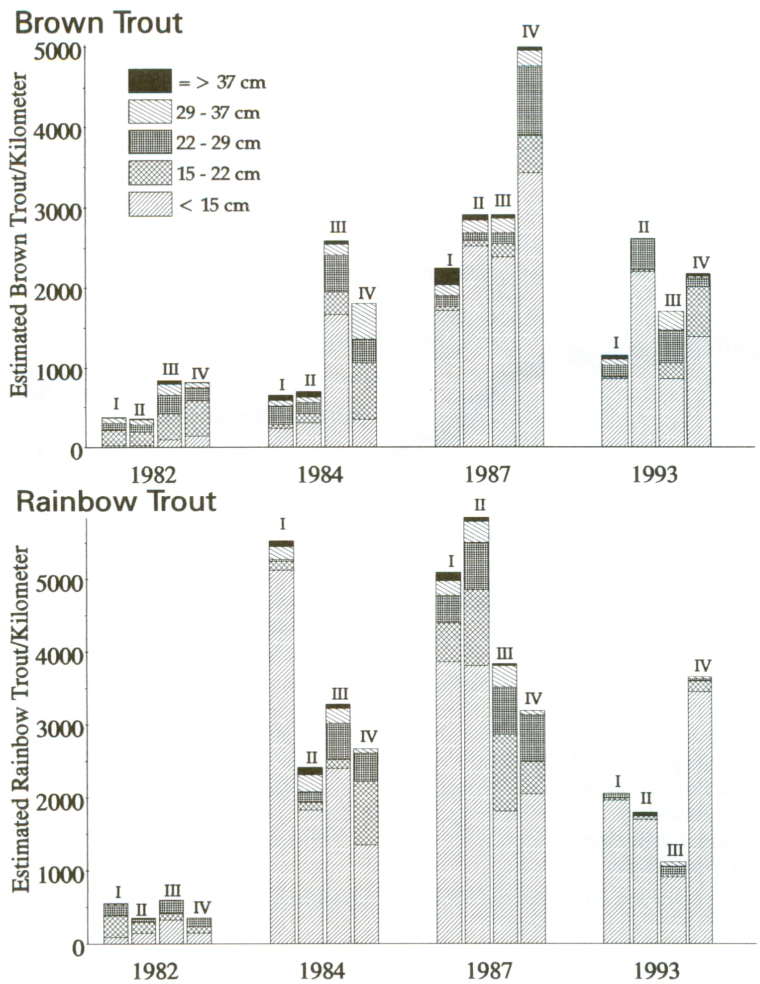

FIGURE 5.—Estimated numbers of trout per kilometer by size-class at four sites on the Truckee River. Roman numerals (I–IV) coresond to study sites in Figure 4.

had made frequent purchases from the parasite-positive northern California grower and made multiple distributions into southern California waters.

There is little evidence that infected anadromous stocks are contributing to the spread of *M. cerebralis* in California. Infected RT stocks are known in five coastal streams and rivers entering directly into the Pacific Ocean in Monterey, Santa Cruz, and San Mateo counties. Since the original discovery at Garrapata Creek in 1965, only a small number of coastal streams remain positive for the parasite. Straying anadromous fish do not appear to be spreading the parasite into 20 nearby coastal waters tested to date, and the parasite is no longer detected at Garrapata Creek.

In 1985, approximately 388,000 *M. cerebralis*-positive RT were released from the CFH into the upper Sacramento River near Red Bluff, California (J. Ruth, U.S. Fish and Wildlife Service, personal communication). The Sacramento River runs south through San Francisco Bay, allowing ample opportunity for infected returning adults to stray and spread infection into RT populations inhabiting local San Francisco Bay area streams. Since the release in 1985, intensified sampling efforts have failed to detect *M. cerebralis* in 18 anadromous fish streams entering directly into San Francisco Bay.

Impacts

Nonquantitative empirical observations of wild salmonid populations in *M. cerebralis*-positive wa-

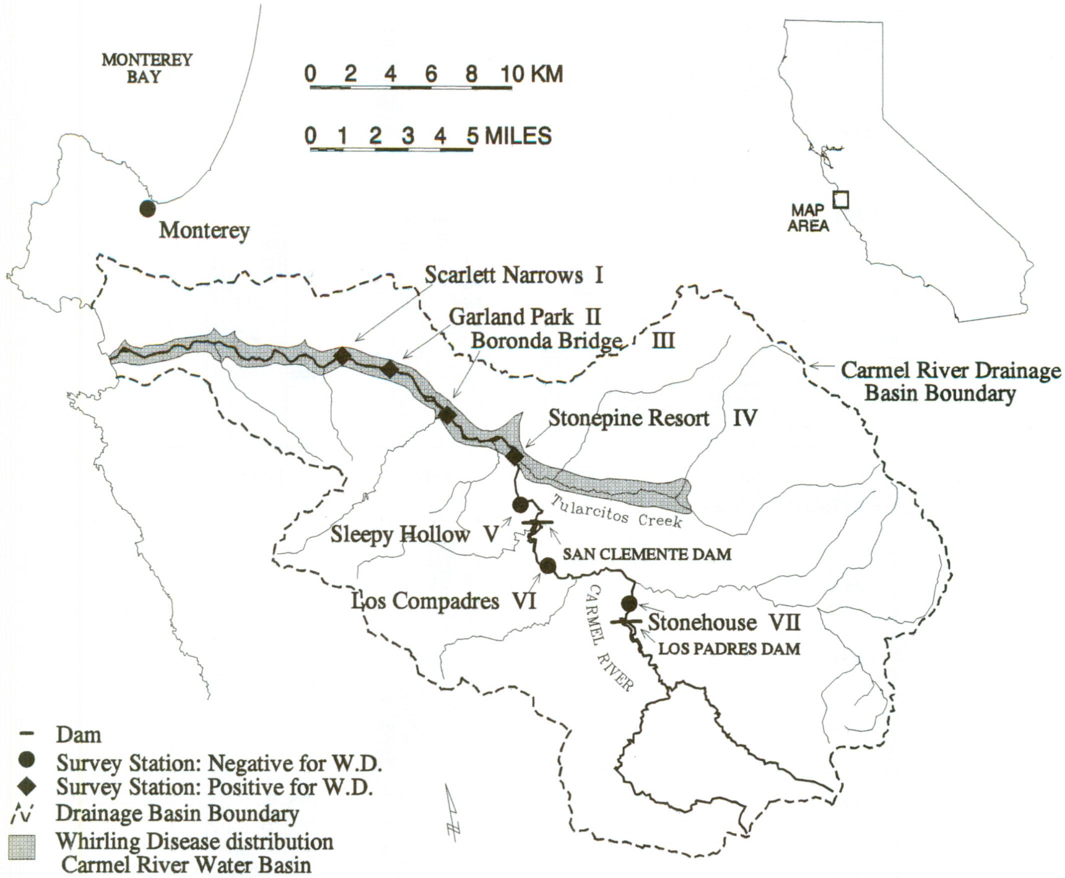

FIGURE 6.—Seven fish population study sites (I–VII) in the Carmel River basin, California (W. D. = whirling disease).

ters by CFG fishery biologists and Fish Health Laboratory staff between 1965 and 1997 do not support a relationship between depressed fish population numbers and *M. cerebralis* in California waters. Population data comparing RT and BT populations in Sagehen Creek (Ermin 1986), age-class composition of RT and BT in the lower Truckee River (J. Deinstadt et al., CFG, unpublished data), and RT population densities in *M. cerebralis*-positive and -negative sections of the Carmel River (D. Dettman, MPWMD, personal communication) appear to confirm this conclusion.

Fish population data (Erwin 1986) comparing 1982 RT and BT population densities with the 1952–1961 period average at nine stations along a 13-km section of Sagehen Creek suggest no indication of a significant RT and BT population decline in *M. cerebralis*-positive waters of Sagehen Creek (Figures 2, 3). Population densities found in the lower sections (sites VI through IX) cohabited by both RT and BT did not suggest RT were being adversely affected by the presence of *M. cerebralis.* Although significantly lower in 1982 than 1951–1962 at station VI, RT population densities remained nearly unchanged at stations VII and VIII and were significantly higher at section IX in 1982 than the 1952–1961 average.

Myxobolus cerebralis has been known to occur in the Truckee River since the mid-1960s and has been found routinely in both RT and BT populations by CFG pathologists. Observations during the 11-year period of 1982–1993 indicated a healthy recruitment of younger age-class RT and BT to larger year-class sizes during most years (Figures 4, 5). The low recruitment of RT to larger age-classes in 1993 is thought to be related to drought and low water conditions and velocities that prevailed between 1987 and 1992, which favored BT populations. The nearly 30-year history of *M. cerebralis* in the Truckee River does not

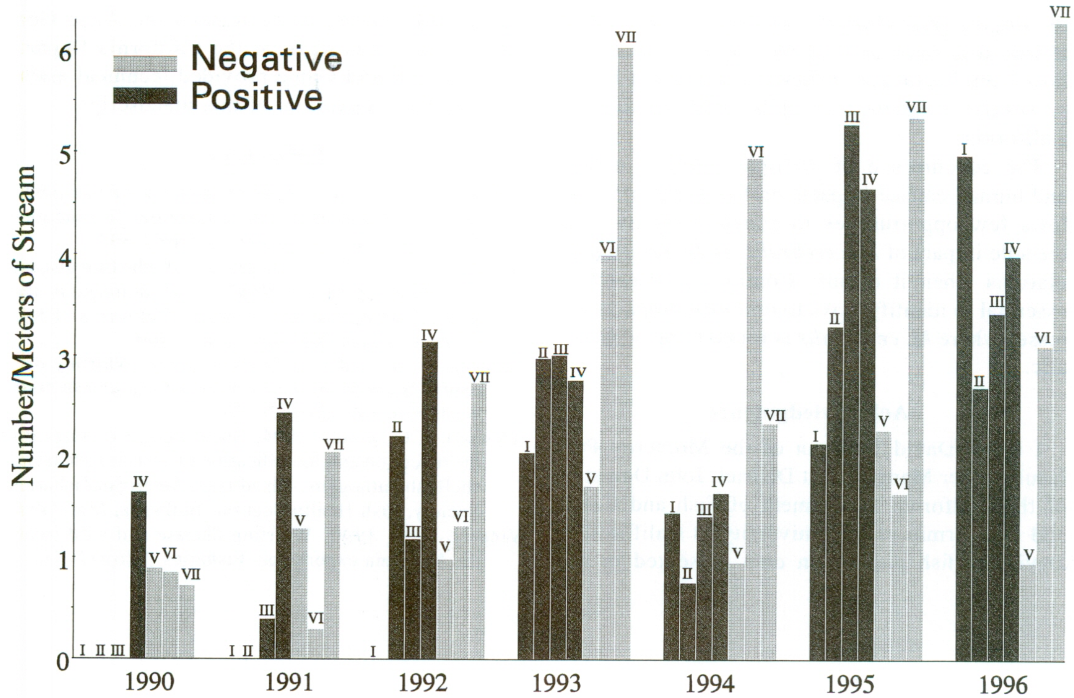

FIGURE 7.—Average lineal densities (number of fish per meter of stream) juvenile steelhead at seven sites along the Carmel River, 1990–1996. Shading indicates absence (negative) or presence (positive) of *M. cerebralis* at a site. Roman numerals (I–VII) correspond to study sites in Figure 6.

appear to have affected RT year-class recruitment in 1984 and 1987, when significant numbers of larger age-class RT were reported. Lower numbers of both RT and BT reported in 1982 are thought to be due to heavy flooding during the winter and spring of 1982.

Steelhead (anadromous rainbow trout) population data collected by the MPWMD on the Carmel River in Monterey County during a 7-year period (1990–1996) show no clear correlation between RT numbers and the presence of *M. cerebralis* (Figures 6, 7). Seven sampling stations were located on a 26-km section of the river within 40 km of the Pacific coast. The lower four stations (I–IV: Scarlett Narrows, Garland Park, Boronda Bridge, and Stonepine Resort) located below the Tularcitos Creek tributary have consistently been positive for *M. cerebralis* throughout many years of sampling. Three stations above Tularcitos Creek (V through VII: Sleepy Hollow, Los Compadres, and Stonehouse) have never been found positive for the parasite. Although RT numbers vary considerably from year to year, there appears to be little or no correlation between population numbers determined at the four lower (positive) and the three upper (negative) sampling sites. No data were reported for the lower sampling stations in 1990, 1991, and 1992 due to drought conditions and lack of surface water at those stations.

Conclusions

Myxobolus cerebralis has become widely established in native salmonid species in a number of western states since its discovery in California in the mid-1960s. Despite its wide distribution, there is little clear evidence of significant impacts on wild salmonids in California. In some waters, skeletal anomalies symptomatic of WD occur that are not clearly related to depressed population numbers. Thirty-two years have passed since the initial discovery of *M. cerebralis* in California. In that time the anticipated severe economic and environmental impacts from this parasite to the valuable fishery resources of California have not materialized. The significant impacts reported in Montana and Colorado may result when environmental conditions favor large tubificid worm populations as experienced during the devastating 1995 hatchery epizootic at Mt. Whitney. It appears that high gradients, frequent flushing action, and the oligotrophic character common to many California drainages prevent the required alternative host from becoming sufficiently abundant for *M. cerebralis* to significantly affect wild salmonids in California.

The concurrence of multiple negative natural and human-caused impacts on fish populations allows few opportunities to conclusively evaluate the sole impact of *M. cerebralis* on depressed populations when it occurs. Continuing research is essential to identify ways to minimize impacts and losses where *M. cerebralis* is found to be problematic.

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