The Potential Distribution and Abundance of Zebra Mussels in California

by

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Additional technical information is provided in a companion report:

A. Weinstein and A. N. Cohen, *Methods and Data for Analysis of Potential Distribution and Abundance of Zebra Mussels in California*, Bio-invasions Research Report No. 1, San Francisco Estuary Institute, Richmond CA.

Introduction

This report examines the potential distribution and abundance of the zebra mussel *Dreissena polymorpha* in California. This freshwater mussel has been one of the most harmful biological invaders of North America. Where zebra mussels have become abundant their impacts have included tens of millions of dollars of costs to water delivery systems, the extirpation of populations of native clams and mussels, and large-scale changes in aquatic community structure. Zebra mussels spread quickly through much of eastern North America, but have not yet established populations west of the Continental Divide. However, they have been found on several occasions on trailered boats entering California and, as reported here, many of California's waters, including many of the state and federal water project facilities, could support zebra mussels.

This report provides background on the zebra mussel and its impacts, and describes this study's methods and results. Additional information on the methods used and on the relationship between environmental factors and potential distribution and abundance, anlong with the water quality data used in the analysis, are provided in the technical report noted in the table of Contents (hereafter cited as the *Methods and Data* report).

History of the Zebra Mussel in Europe and North America

Origin and Spread

Zebra mussels were originally restricted to the watersheds of the Black, Caspian, and Aral seas in eastern Europe and western Asia. Shipping canals constructed in the 18th and 19th centuries created connections to other watersheds, and zebra mussels quickly spread across Europe and through the western half of the Soviet Union, more than doubling their range between 1800 and 1900 (Stanczykowska and Lewandowski 1993; Karatayev et al. 1997).

In the 1980s zebra mussels were introduced to the Great Lakes in North America, probably in the ballast water of cargo vessels arriving from European freshwater ports. Ballast water—water pumped in large quantities into cargo holds or dedicated ballast tanks at the start of a voyage in order to achieve proper buoyancy, and later discharged on arrival at a port prior to taking on cargo—has been implicated in the transport and introduction of numerous freshwater, estuarine, and marine species to North America in the last several decades (Carlton 1985, Carlton and Geller 1993). Until recently foreign ballast water was routinely discharged into the Great Lakes as ships took on cargo. McMahon (1996) has also suggested that zebra mussels could have been introduced into the Great Lakes as adults attached to anchors or chains.

Within three to five years of the first North American sighting, zebra mussels had spread throughout all five Great Lakes and overland to the Susquehanna and Hudson rivers in New York. By the end of 1996, zebra mussels had invaded waters in 20 states and two Canadian provinces, as far west as the Oklahoma River and as far south as New Orleans (Ram and McMahon 1996).

A related mussel, called the quagga mussel (*Dreissena bugensis*), was apparently also introduced into Lake Ontario in the late 1980s. Its range now includes eastern portions of the Great Lakes Basin and the freshwater portions of the St. Lawrence River (Fig. 1). Quagga and zebra mussels differ in some physiological and life history characteristics. For example, quagga mussels settle and thrive in deeper and colder water than zebra mussels and can settle on soft substrates, but have less tolerance for exposure to air and high salinities (Mackie and Schloesser 1996; McMahon

1996). However, since these differences are relatively minor, and there is much less information available on quagga mussels, the analysis in this report is based entirely on zebra mussels.

Ecological and Economic Effects

Zebra mussels have become costly fouling pests in both Europe and North America. The greatest economic damage has occurred when zebra mussels infest the filters, pipes, pumps, or other components of municipal and industrial water delivery systems. Here they find hard substrates to attach to, steady flows of water to bring them food, and protection from predators. Populations can achieve astonishing densities, up to 750,000 individuals per square meter in layers more than a foot thick (O'Neill 1996a). This is many times greater than the highest densities ever observed in Europe (Ramcharan et al. 1992).

Early estimates projected that zebra mussel prevention, control, and monitoring would cost raw-water facilities in the Great Lakes region a total of 2-5 billion dollars by the late 1990s (Office of Technology Assessment 1993). Recently, O'Neill (1996b) surveyed costs associated with zebra mussel control, prevention, and research at about one-sixth of affected facilities in the United States and Canada from 1989-1995. The 339 facilities, ranging from small businesses to large power plants, reported cumulative costs of just over $69 million for the six-year period, with 51% of the costs incurred by power plants, 31% by water treatment plants, 8% by industries, 7% by public agencies, and 1% by scenic riverways.

Where abundant, zebra mussels have had a variety of ecological impacts on invaded waters. First, they dramatically alter natural communities by shifting plant production from pelagic (in the water column) to benthic (bottom) zones of lakes and large rivers. Zebra mussels have greatly reduced populations of phytoplankton (microscopic drifting plants that are an important component of aquatic food webs), even in the largest lakes. For example, phytoplankton were reduced by 60% in Lake Erie and 90% in the Hudson River following the establishment of large populations of zebra mussels. The removal of phytoplankton, bacteria, and suspended sediments can greatly increase water clarity, which in some areas has led to an explosive increase in bottom-growing algae (Leach 1993; Karatayev et al. 1997).

Second, zebra mussels have altered the abundance of zooplankton (microscopic drifting animals) and benthic invertebrates. For example, the abundance of small rotifers (a type of zooplankton) in western Lake Erie fell 75% following the establishment of large populations of zebra mussels, which suppress small zooplankton by eating both the zooplankton and their food (Leach 1993). Reduced zooplankton populations can lead to reduced populations of fish, such as yellow perch, whose larvae subsist on zooplankton. The commercial catch of yellow perch in Saginaw Bay has declined precipitously in the past several years, simultaneous with a rise in zebra mussel abundance and a two-thirds decrease in the abundance of the perch's zooplankton food (Jude 1996). In contrast, the abundance and diversity of benthic invertebrates tends to increase in the presence of high densities of zebra mussels, whose mats of shells greatly enhances the amount of habitat available to small crustaceans, snails, and other animals. The populations of crayfish and some worms, which prey on these animals, in turn increases (Karateyev et al.1997).

Third, zebra mussels can contribute to the transfer and concentration of toxic contaminants in food chains, by accumulating metals and organochlorines in their tissues at levels up to 100,000 times the concentration in the surrounding water column. For example, researchers found higher levels of several organic contaminants in diving ducks that had fed on Lake Erie zebra mussels than in ducks that had not (de Kock and Bowner 1993). If taken in sufficient amounts, some of these contaminants can cause reproductive damage such as increased embryo mortality, reduced egg size, and nest abandonment.

Finally, zebra mussels pose a direct threat to the nearly 300 species of native freshwater bivalves (clams and mussels) in North America, many of which are already rare or declining. Zebra mussels apparently prefer settling on bivalve shells over other substrates, and can accumulate in sufficient numbers to smother the host. Dense populations of zebra mussels can also starve native bivalves by consuming the plankton. By 1992 native bivalve populations were reduced to low numbers in western Lake Erie, and many had been eliminated from southern Lake St. Clair. In the United States, all bivalve species coexisting with zebra mussels suffer from at least low to medium levels of infestation (Schloesser et al. 1996). In Europe, however, after dramatic declines in the abundance of native bivalves during the early stages of zebra mussel invasion, populations have now stabilized (Karateyev et al. 1997). Also, no European freshwater native bivalve is known to have been extirpated from any lake by zebra mussels.

Potential Introduction and Impacts in California

Possible Means of Introduction

Zebra mussels can reach uncolonized waters either through natural dispersal or through human-mediated transport. Natural dispersal could occur through drifting larvae, adults attached to floating objects, or eggs, larvae or adults carried by animals such as turtles or ducks. Human-mediated transport—including transport in ships' ballast water, on boat or barge hulls, in live wells on trailered boats, in shipments of commercial aquatic plants or bait, or by other means—can potentially move mussels across hundreds to thousands of miles, and over barriers to natural dispersal, such as oceans or dry or mountainous terrain.

Three general modes of movement contribute to zebra mussel range expansion: (1) *Progressive spread through connected waterways*. Primary mechanisms include downcurrent movement as drifting larvae, and both upcurrent and downcurrent movement as adults attached to the hulls of boats and barges. Downcurrent movement, and upcurrent movement within navigable waters, can be quite rapid, as it was through the Great Lakes and the major waterways of the Mississippi Basin. (2) *Stepping-stone spread between isolated water bodies*. This involves movement over drainage divides, which can occur through human-mediated transport (on trailered boats, in bait buckets) or less commonly by natural means (attached to birds, turtles, or other animals). By either means, this form of expansion tends to be sporadic and slow. For example, by 1996 zebra mussels had been found in only 40 of the 2000 large (over 100-acre) isolated inland lakes in Michigan (3) *Long-distance leaps*. This is most likely to occur through transport on trailered boats or in ships' ballast. Generally, such events are sporadic and unpredictable (Johnson and Padilla 1996; Carlton and Geller 1993).

Zebra mussels are currently found only in waters east of the Continental Divide, making spread to California through connected waterways impossible. Stepping-stone spread has been sporadic and slow even among the clustered waters of the Midwest. Greater distances between suitable water bodies, more arid conditions, and fewer trailered boats moving between waterways would make stepping-stone spread across the West even slower and less likely. Given these physical limitations, the most promising way for zebra mussels to reach California in the near future is through a human-mediated, long-distance leap. A few different mechanisms might allow such a leap:

Trailered boats. In 1993, at the urging of the California Department of Water Resources, the California Fish and Game Commission banned the transport of live zebra mussels into the state. The California Department of Food and Agriculture then began inspecting trailered boats entering the state, and soon found a cluster of dried zebra mussels on a boat arriving from the Great Lakes.

By 1996, inspectors had found zebra mussels on 13 boats; in two cases the mussels were undesiccated and may have been alive (J. Janik 1997). Since inspectors primarily check for adults attached to boat hulls, within the first few inches of engine pipes, and in wet areas within the boat, they would possibly miss eggs or larvae, as well as adults attached deeper within the pipes. Boats that are found to have zebra mussels must be cleaned and reinspected by the California Department of Fish and Game before they are allowed to enter State waters (D. Peterson, pers. comm. 1997).

It has been reported that adult zebra mussels can survive out of water for 4-21 days under certain conditions, and that larvae in baitwells can survive 3-5 days (Carlton 1993; Johnson 1997). Travel time from the zebra mussel's current range to the Sacramento-San Joaquin Delta at an average speed of 55 mph is about 35 hours. It therefore seems that zebra mussels could, at least on occasion, survive the journey and be released alive in California waters. However, unless a relatively large number of mussels are introduced into a relatively small body of water, the dispersal of the mussels' planktonic larvae by water currents may make it unlikely that the larvae will settle close enough to each other to allow successful spawning and fertilization. Given that successful overland spread even over short distances in the Midwest has been relatively rare, the chances of accidentally carrying zebra mussels nearly 2,000 miles over arid terrain, and then inoculating them into an appropriate water body in adequate quantities to establish a new population, may be quite low.

Ballast water. In recent decades a number of organisms, including some from the North Atlantic region, have been introduced into the San Francisco Estuary via ballast water (Cohen and Carlton 1995). Each year about 20-30 ships arrive in the Estuary whose last port of call is in Europe or eastern North America (Carlton et al. 1995; Marine Exchange 1996). Some of these may include freshwater ports with zebra mussel populations. As a ship can carry ballast water not only from its last port, but also from previous ports, the number of ships potentially carrying zebra mussels into the Estuary may be somewhat larger.

Zebra mussels carried to California in ballast water would have a reasonable chance of becoming established only if released into fresh or mildly brackish waters in the Sacramento-San Joaquin Delta, or in some years, Suisun Bay (although an initial introduction to the Pacific Coast could also occur at ports on the Columbia River). While this is probably not a common occurrence, in 1995 at least one ship arrived in the Delta from New Orleans, where zebra mussels are abundant (S. Gibbs, pers. comm. 1997). In contrast to trailered boats, there is currently no effort to monitor or control this invasion pathway. Mandatory mid-ocean ballast water exchange, similar to that required for the Great Lakes and the Port of Vancouver in British Columbia, could virtually eliminate the possibility of a zebra mussel invasion via ballast water.

Other mechanisms. There is potential for bringing in zebra mussel larvae in the water used to transport fish or aquatic plants into California. At least one commercial baitfish operator transports fish to California from the Oklahoma River, where there are zebra mussels (J. Janik, pers. comm. 1997). No systematic study has been done of the sources of baitfish and stocked fish arriving in California and the fate of the water holding the fish. The three largest dealers of plants for aquaria and ornamental ponds are based in Ohio, which has zebra mussels. Sales of these plants could quickly transport zebra mussel adults, larvae, or eggs among states. (S. Nichols, pers. comm. 1997). Finally, other activities which have been documented as dispersal mechanisms, such as intentional introductions for novelty or algae control, could bring zebra mussels to California.

Potential Impacts

The zebra mussel could have very significant economic and ecological impacts in California, potentially even more serious than in the American Midwest. In the Midwest, the densest concentrations of zebra mussels are found within the plumbing of water delivery systems and in the cooling water systems for power plants. Should zebra mussels be introduced into California, hundreds of reservoirs and thousands of miles of steel and concrete pipes, water gates, fish screens, water intakes, filter plants, agricultural irrigation systems, and many other water system components could be at risk. The State Water Project and the Central Valley Project alone have over 1600 miles of aqueducts and canals (J. Janik 1997). Virtually every citizen and agency in California is directly or indirectly dependent upon these systems to provide water for households, businesses, and agriculture.

Abundant zebra mussel populations could reduce or eliminate populations of rare species, change the composition of biotic communities, and alter the physical and chemical conditions of aquatic habitats. California has one of the highest concentrations of rare freshwater fish, amphibians, and aquatic invertebrates of any state in the country, many of which already suffer from the impacts of pollution, habitat fragmentation, and introduced species. In the San Francisco Estuary, a recently introduced Asian clam (*Potamocorbula amurensis*) has eliminated phytoplankton blooms in the northern part of the Estuary, so that many zooplankton and benthic organisms in this region now survive on organic matter carried in from the Sacramento-San Joaquin Delta. If zebra mussels were to become abundant in the Delta and Central Valley rivers, and efficiently filter the organic material out of these waters as they have in parts of the Great Lakes, there might be little left for organisms in the northern Estuary to feed on.

Methods

Previous Studies of Potential Distribution and Abundance

Investigators have assessed the risks of zebra mussel invasions in terms of three concepts whose definitions vary somewhat throughout the literature. *Colonization potential* is the suitability of a water body to support a reproducing zebra mussel population. European and North American studies suggest that colonization potential is primarily controlled by calcium, pH, temperature, and salinity. *Potential abundance* in waters suitable for colonization is controlled by these and other physical and biological factors. The *vulnerability* of a water body includes both its suitability for colonization and its exposure to natural and human-mediated means of introduction. For example, a reservoir popular with boaters and anglers may be more vulnerable than a less-used reservoir.

Following the invasion of zebra mussels in North America, efforts have been made to assess the colonization potential of various regions. Strayer (1991) used air temperature, water hardness, and river geomorphology to estimate the potential range of zebra mussels across North America, and concluded that most of the United States and much of southern Canada are suitable (having a moderate to high colonization potential). He classified most of California, except for the hot southeastern portion of the state, as suitable. Strayer emphasized, however, that inhospitable water chemistry could prevent colonization of certain areas within the predicted range, and that acclimation to higher temperatures could expand colonization outside of this range.

Neary and Leach (1991) analyzed over 6000 inland lakes in Ontario for both colonization potential and vulnerability using pH, calcium levels, and road access data, and concluded that most of the accessible lakes are too poor in calcium to support zebra mussels. Strayer and Smith (1993) reviewed zebra mussel distribution relative to salinity in European estuaries, and speculated that mussels could become moderately to highly abundant in the Hudson River Estuary in New York state. Murray et al. (1993) assessed Connecticut waters and concluded that low calcium levels would prevent colonization in much of the state. Koutnik and Padilla (1994) examined 154 large lakes in Wisconsin and concluded that nearly half of these lakes were too low in calcium to support zebra mussels. In Virginia, Baker et al. (1995) found the colonization potential of lakes, rivers, and estuaries to be limited by calcium and salinity. Jeff Janik and Dan Peterson of the California

Department of Water Resources considered three sites along the California Aqueduct in 1995 and found calcium, pH, and temperature ranges to be suitable for zebra mussel colonization (Janik 1997). Doll (1996) examined calcium, pH, temperature, dissolved oxygen, and salinity levels in North Carolina, and concluded that most inland waters are too calcium-poor, and most coastal waters too salty, to support zebra mussels. Finally, Hayward and Estevez (1997) examined over 9,000 locations in Florida and concluded that most waters are too turbid and low in calcium and pH to support zebra mussels.

Relating zebra mussel abundance to environmental variables has proved more difficult, in part because of the apparent importance of a larger number of chemical, physical, and biological factors. Strayer (1991), in an analysis of 44 European studies, found significant but weak correlations between densities and temperature or rainfall and concluded that "it is not possible on the basis of available data to predict the density of *D. polymorpha* from environmental data." Ramcharan et al. (1992), however, found that in 76 European lakes, zebra mussel densities decreased as levels of certain algal nutrients rose above or fell below moderate levels, suggesting that lakes that are either eutrophic (having high levels of nutrients) or oligotrophic (having low to no levels of nutrients) provide poor habitat for zebra mussels. They offered two models for predicting densities, one based on pH, calcium, phosphate and nitrate levels, the other based on pH and phosphate only. Mellina and Rasmussen (1993) investigated the influence of substrate type on density in Canadian rivers and lakes, and found that zebra mussels became more abundant as substrate grew coarser, and that substrate size explained 40% to 90% of the observed variation in density. The *Methods and Data* report provides more detailed information and references on factors affecting distribution and abundance.

Method of Analysis

In this study we analyzed and mapped the colonization potential of zebra mussels at a number of sites in California, based on a selected set of environmental variables. We also considered how additional factors may affect colonization potential and abundance.

We reviewed what is known regarding the environmental variables and tolerance ranges that limit zebra mussel distribution through a reading of the published literature and discussions with zebra mussel researchers. There is general agreement that certain water chemistry variables are strong predictors of colonization potential, meaning that zebra mussels should be able to colonize waters where these variables fall into known physiological tolerance ranges. Generally, zebra mussels require an environment that is rich in calcium, fresh to mildly brackish, warm-to-cool, and alkaline, and require flow speeds that are low enough to allow young to settle and adhere. Some of these requirements are different during the active reproductive months of the spring and summer. For example, adult mussels can tolerate pH levels of as low as 7.0, while juveniles need more alkaline conditions, of at least pH 7.4 (McMahon 1996).

We based our analysis on five environmental variables for which tolerance limits are well-studied and data are available: salinity, dissolved calcium, pH, temperature, and dissolved oxygen. For most variables, we used averaged data for April to September to capture conditions during the zebra mussel's spawning and growth period. We classified waters as having high, moderate, or low-to-no colonization potential based on their habitat suitability across all five variables, giving greater weight to calcium and pH, and mapped the results. In some cases we incorporated other information, such as records of periodic desiccation of shallow lakes, in our assessment.

We selected 160 sampling locations for analysis, including rivers, lakes, reservoirs, aqueducts, and canals, basing our selection in part on the availability of data. We chose sites to cover most of the state, capture a wide range of water quality conditions, show elevational changes along rivers, and include the large water delivery systems. The primary source of data was STORET, the U. S.

Environmental Protection Agency's (EPA) water quality data clearinghouse, which consolidates and organizes water quality data from federal, state, and local agencies. Eric Wilson, the STORET manager for EPA Region IX, extracted and tabulated the data for this study. We also obtained data from the California Department of Water Resources, the Regional Water Quality Control Boards (Regions 6 and 7), the City and County of San Francisco, the Metropolitan Water District, the Los Angeles Department of Water and Power, the East Bay Municipal Utility District, the Contra Costa Water District, and the Tahoe Research Group. The *Methods and Data* report provides a more detailed description of the methods along with the data used in the analysis.

Results

Potential Distribution

The zebra mussel has a wide but not comprehensive potential range in California (Figure 2). Of the 160 sites that we assessed, 54% ranked as having low or no potential for colonization by zebra mussels, 2% ranked as having moderate potential, and 44% ranked as having high potential (Table 1). Most of the coastal watersheds, the west side of the Sacramento Valley, and the San Joaquin River and southern Delta, provide suitable water chemistry and temperature for colonization. Suitable waters include many important facilities such as the Delta-Mendota Canal, the California and South Bay aqueducts, the Los Angeles Aqueduct, the Colorado River Aqueduct, the All American Canal, and their associated reservoirs.

Of the 86 sites we ranked as having low or no colonization potential, low calcium was the critical factor in 65% of the sites, a combination of low calcium and low ph in 17% of the sites, high temperature in 12% of the sites, periodic desiccation in 5% of the sites, and low temperature or high salinity at the remaining 1% of the sites. Low calcium, sometimes combined with low pH, will prevent significant zebra mussel colonization in most of the Sierra Nevada and the upper Sacramento River watershed. Warm summer temperatures will prevent colonization at several southern California sites. Freezing, which is thought to limit zebra mussels' range in parts of Europe, may prevent establishment in small or shallow lakes in California that freeze solid in the winter, though no such lakes were included in this assessment.

Periodic desiccation, possibly combined with high or fluctuating salinities, will prevent establishment in some northeast lakes. Zebra mussels can tolerate salinities up to about 8 parts per thousand (ppt) as long as changes in salinity are gradual, so they may be able to colonize some inland brackish waters, although others, such as Mono Lake and the Salton Sea, are clearly too salty. Zebra mussels' low tolerance for rapidly changing salinities would limit their seaward distribution in estuaries and coastal lagoons. They are abundant in some slightly brackish water portions of estuaries in Europe, but seldom persist where salinity exceeds 2 ppt. We therefore estimate that zebra mussels could colonize in the Bay/Delta Estuary downstream to a tide-averaged, near-bottom salinity of 2 ppt (a position in the Estuary that researchers describe by the variable X2 [Kimmerer and Monismith 1992]), or roughly to near Antioch in dry years and to Honker or Grizzly bays, and occasionally even further downstream, in wet years. Here and throughout coastal California, rapidly fluctuating salinity levels would make many tidal regions very unstable habitats for zebra mussels, and their presence would likely depend on an upstream source of larvae to reestablish extirpated colonies.

Table 1.

Zebra Mussel Colonization Potential at 160 sites in California

1	Alamo River near Calipatria	low-to-no
2	All American Canal	high
3	American River at Nimbus Dam	low-to-no
4	American River near Carmichael	low-to-no
5	Anderson Reservoir at dam	high
6	Antelope Lake	low-to-no
7	Arroyo Seco near Soledad	high
8	Bear River near Wheatland	low-to-no
9	Black Butte Reservoir	high
10	Butte Creek near Chico	low-to-no
11	Cache Creek near Lower Lake	high
12	Calero Reservoir near New Almaden	high
13	California Aqueduct near Check 21	high
14	California Aqueduct at Check 41	high
15	California Aqueduct near Kettleman	high
16	Camanche Reservoir	low-to-no
17	Carmel River near Carmel	high
18	Chowchilla River below Buchanan Dam	high
19	Clear Lake–upper arm	high
20	Clear Lake–lower arm	high
21	Clifton Court	high
22	Colorado River at Aqueduct intake	high
23	Colorado River Aqueduct–Lake Mathews	high
24	Contra Loma Reservoir	high
25	Cosumnes River at Michigan Bar	low-to-no
26	Coyote Creek below Anderson Dam	high
27	Crystal Springs Reservoir	low-to-no
28	Delta Mendota Canal 2.2 mi S of Firebaugh	high
29	Delta Mendota Canal at head	high
30	Don Pedro Reservoir at influent	low-to-no
31	Lake Sonoma–Dry Creek Arm	low-to-no
32	Eagle Lake	low-to-no
33	East Highline Canal	high
34	Eel River at Scotia	high
35	Eel River near Dos Rios	high
36	Eel River at Black Butte River	high
37	Eel River South Fork Near Miranda	high
38	Russian River near Ukiah	moderate
39	Feather River Middle Fork near Portola	low-to-no
40	Feather River near Nicolaus	low-to-no
41	Folsom Lake near Folsom	low-to-no
42	Frenchman Lake	low-to-no
43	Fresno River near Daulton	moderate
44	Friant-Kern Canal at Friant	low-to-no
45	Glenn-Colusa Canal near Hamilton City	low-to-no
46	Goose Lake	low-to-no
47	Hetch Hetchy Reservoir	low-to-no
48	Honey Lake	low-to-no
49	Indian Valley Reservoir	high
50	Iron Canyon Reservoir	low-to-no
51	Kaweah River at Three Rivers	low-to-no
52	Kaweah River below Terminus Dam	low-to-no
53	Kern River above Fairview	low-to-no
54	Kern River near Bakersfield	low-to-no
55	Kings River near Trimmer	low-to-no
56	Kings River–South Fork at Cedar Grove	low-to-no
57	Klamath River at Hamburg	low-to-no
58	Klamath River near Klamath	high
59	Klamath River at Orleans	low-to-no
60	Klamath River below Iron Gate Dam	low-to-no
61	Lake Almanor–east arm	low-to-no
62	Lake Britton at Ferry Crossing	low-to-no
63	Lake Castaic	high
64	Lake Davis	low-to-no
65	Lake Del Valle at Glory Hole	high
66	Lake Perris at inlet	high
67	Lake Tahoe	low-to-no
68	Lake Berryessa at dam	moderate
69	Lake Havasu at Parker Dam	low-to-no
70	Lake Isabella at Engineer Point	low-to-no
71	Lexington Reservoir at dam near Los Gatos	high
72	Lower Alkali Lake	low-to-no
73	Los Angeles Aqueduct–Grant Lakes	low-to-no
74	Los Angeles Aqueduct–Merritt Cut	high
75	Los Angeles Aqueduct–Tinemaha	high
76	Los Angeles River at Long Beach	low-to-no
77	Mad River near Arcata	high
78	Mammoth Creek at Highway 395	low-to-no
79	Mariposa Creek below Mariposa Dam	high
80	McCloud Reservoir at dam	low-to-no
81	McCloud River above Shasta Lake	low-to-no
82	Merced River near Stevinson	low-to-no
83	Merced River–South Fork near El Portal	low-to-no
84	Stanislaus River–Middle Fork at Dardanelle	low-to-no
85	Millerton Lake near Friant Dam	low-to-no
86	Mojave River near Victorville	low-to-no
87	Mokelumne River at Woodbridge	low-to-no
88	Mono Lake	low-to-no
89	Nacimiento Reservoir–lower arm	high
90	Napa River near Napa	high
91	New River at international boundary	low-to-no
92	North Bay Aqueduct at Barker Slough	high
93	Old River at Tracy Road Bridge	high
94	Old River Intake	low-to-no
95	Owens River below Tinemaha	high
96	Pajaro River at Chittenden	high
97	Pardee Reservoir	low-to-no
98	Pillsbury Lake near Potter Valley	high
99	Pine Flat Reservoir above dam	low-to-no
100	Piru Creek release from Pyramid Dam	high

Table 1 continued.

Zebra Mussel Colonization Potential at 160 sites in California

101	Pit River–South Fork near Likely	low-to-no
102	Pit River near Canby	high
103	Pit River near Montgomery Creek	low-to-no
104	Putah Creek below Monticello Dam	high
105	Pyramid Lake at inlet	high
106	Rock Slough at Plant	low-to-no
107	Sacramento River at Delta	low-to-no
108	Sacramento River at Freeport	low-to-no
109	Sacramento River at Keswick	low-to-no
110	Sacramento River near Red Bluff	low-to-no
111	Salinas River near Bradley	high
112	Salinas River near Chualar	high
113	Salmon River at Somesbar	low-to-no
114	Salton Sea–midpoint near County Line	low-to-no
115	San Andreas Reservoir	low-to-no
116	San Antonio River below San Antonio Dam	high
117	San Antonio Reservoir	high
118	San Benito River near Willow Creek School	high
119	San Diego River at El Capitan Dam	high
120	San Gabriel River at Azusa	high
121	San Joaquin River at Antioch Ship Channel	high
122	San Joaquin River near Stevinson	high
123	San Joaquin River at Highway 152 Bridge	high
124	San Joaquin River Below Friant Dam	low-to-no
125	San Joaquin R–S Fork at Mono Hot Springs	low-to-no
126	San Lorenzo River near Boulder Creek	high
127	San Luis Reservoir at trashracks	high
128	San Luis Rey River at Oceanside	low-to-no
129	San Pablo Reservoir	high
130	Santa Ana River at MWD Crossing	low-to-no
131	Santa Clara River at LA-Ventura Co. line	high
132	Santa Ynez River at Narrows near Lompoc	high
133	South Bay Aqueduct at Santa Clara Terminus	high
134	Scott River near Fort Jones	high
135	Sespe Creek near Fillmore	high
136	American River–South Fork near Lotus	low-to-no
137	Shasta Lake near Shasta Dam	low-to-no
138	Shasta River below Dwinnell Reservoir	low-to-no
139	Silverwood Lake at San Bernardino	high
140	Siskiyou Lake–upper end near Shasta City	low-to-no
141	Smith River near Crescent City	low-to-no
142	South Bay Aqueduct at Mile 16.27	high
143	South Bay Pumping Plant	high
144	South Yuba River near Cisco	low-to-no
145	Stanislaus River at Ripon	low-to-no
146	Tehama-Colusa Canal near Red Bluff	low-to-no
147	Thermalito Afterbay	low-to-no
148	Thomes Creek at Paskenta	low-to-no
149	Trinity River at Hoopa	high
150	Trinity River at Lewiston	low-to-no
151	Trinity River near Burnt Ranch	low-to-no
152	Truckee River at Farad 15	low-to-no
153	Tule River below Success Dam	high
154	Tuolumne River at La Grange Bridge	low-to-no
155	Tuolumne River at Modesto	low-to-no
156	Upper Alkali Lake	low-to-no
157	Upper San Leandro Reservoir	high
158	Van Duzen River near Bridgeville	high
159	Whiskeytown Reservoir at dam	low-to-no
160	Yuba River near Marysville	low-to-no

Several cautions apply to these results:

- Additional factors may limit colonization. For example, zebra mussels are usually not found in very productive (that is, having high levels of phytoplankton) or very unproductive waters. Young zebra mussels also need a hard surface on which to settle when moving from the floating larval to the attached adult stage, so waters with mud, clay, or fine sand bottoms may not support zebra mussels. Also, young zebra mussels cannot settle in fast currents.
- The average values for some variables at some sites were just under or just over the tolerance limits used in the analysis. Where these average values were based on a small number of sampling events, especially for calcium or pH, this could have produced a misclassification.
- Interactions of some of the variables may limit colonization. For example, zebra mussels' salt tolerance and metabolic efficiency decrease as temperatures rise beyond 25-28° C; therefore, zebra mussel distribution may be more restricted in the warm southern areas of the state than indicated by our analysis, which did not take such interactions into account.
- Confounding factors in studies of existing zebra mussel distributions may have given us an unrealistically narrow impression of their environmental tolerances; and introduced populations may become adapted, through natural selection and genetic change, to conditions that earlier generations could not tolerate. These issues could lead to waters being judged environmentally unsuitable which later support thriving populations of zebra mussels, as has happened on occasion.

Finally, our preliminary assessment of data on the distribution of zebra mussels in North America and Europe that we acquired late in this study suggests that the calcium levels required for reproduction or early development may be higher than the threshold levels cited by most of the literature and researchers and that we used in this analysis. Should this turn out to be the case, a number of the sites that we classified as suitable habitat may in fact not be able to support *in situ* reproducing populations. Some of these sites, however, could still support dense accumulations of zebra mussels resulting from the settlement of larvae produced by upstream populations. For example, using the highest possible calcium threshold value that is consistent with the distribution data, most waters north of the Bay/Delta region and the Los Angeles Aqueduct would not be susceptible to zebra mussel invasion; the San Joaquin River, Colorado River and most of the Coast Range watersheds from Santa Cruz County southward could still support reproducing populations; and the California Aqueduct, South Bay Aqueduct, Delta-Mendota Canal, Colorado River Aqueduct, and associated facilities could support the settlement and growth of mussels recruited from upstream sites. We hope to sort out the calcium threshold issue with further analysis.

Potential Abundance

Population densities of zebra mussels vary greatly both among waters and within waters over time, and are dependent on many chemical, physical, and ecological factors. The highest known population density—more than 700,000 individuals per square meter—was reported in the pipes of a power plant in the Midwest (O'Neill 1996a). In contrast, zebra mussel densities in European lakes average 1500-4000 individuals per square meter (Stanczykowska and Lewandowski 1993). Zebra mussels tend to be more abundant in waters that are high in calcium, are alkaline, are moderately productive, have plentiful hard substrates, are large and deep, and are still or slowly flowing. Many of California's reservoirs, lakes, aqueducts, and large rivers provide these conditions.

The aqueducts and many of the reservoirs of the State Water Project and the Central Valley Project provide optimal chemical and physical conditions for zebra mussels, and thus may support abundances approaching those seen in the Great Lakes. The California Aqueduct, the Los Angeles Aqueduct, and the Colorado River Aqueduct have concrete or steel substrates and flow rates under 1.5 m/sec (D. Ball, D. Peterson, pers. comm. 1997). Even waters with soft substrates could eventually support high densities of mussels after initially settling on vegetation, sticks, or trash, and then on each other, to form large aggregations. However, flowing water may depress abundance in rivers and streams relative to lakes and reservoirs, and in smaller rivers relative to larger (and generally slower) ones. In Europe, zebra mussels are seldom found in rivers less than 30 meters wide and are generally at least an order of magnitude more abundant in lakes and reservoirs than in large rivers.

Zebra mussel abundance could also be affected by the presence or absence of upstream sources of larvae. Larvae from upstream sources can supplement resident populations and serve to re-inoculate an area should an environmental perturbation, such as a winter die-off, depress or exterminate a population. It is also possible that the settlement of larvae from upstream has created some dense populations in waters that are unsuitable for reproduction.

Finally, abundance may be affected by predation. While it is clear that predation has in some cases significantly depressed the local abundance of zebra mussels, it is not known whether predation could control populations in an entire region and over the long term.

Concluding Thoughts

Our analysis indicates that zebra mussels could survive and thrive in many of California's waters, and that introduction could occur through a variety of pathways, although the levels of risk associated with these pathways are poorly understood. We find that many of the state's most important water delivery facilities would be at risk, and note that the high connectivity of these waterways could promote the rapid spread of zebra mussels within the system.

Zebra mussels' phenomenal success in the Great Lakes Region and their discovery on trailered boats entering California has created the impression that they will soon become established here, and that once here they will spread rapidly and become a major pest. While this scenario may be realized, it is not inevitable. Much may be done that could reduce the risk of zebra mussels' introduction, prevent their spread if they should arrive, and mitigate their impacts should they become established. Such steps could include the following:

- Require mid-ocean exchange of ballast water for ships entering the Sacramento-San Joaquin Delta or upstream sections of San Francisco Bay, and other freshwater ports on the Pacific Coast.
- Require the haulers of trailered boats arriving in California to empty all water from bait wells and flush water from their engine pipes before proceeding.
- Provide information to arriving boaters on the problems associated with zebra mussels, and on how to avoid transporting them.
- Hold any fishing or boating events that are likely to attract participants from east of the Rockies in waters that will not support zebra mussels.
- Identify water bodies that may be likely hotspots for introduction, based on colonization potential and vulnerability (primarily the amount of interstate boat traffic they receive), and focus boater education efforts on these sites. Monitor these sites for the arrival of zebra mussels, and develop containment and eradication plans for them in advance.
- Assess the potential for introducing zebra mussels via commercial baitfish operations, the aquatic plant trade, and other means, and manage as needed.
- Support the efforts of the Western Zebra Mussel Task Force to prevent the westward spread of the zebra mussel.
- In areas of high colonization potential, design any new water system components (including fish screens, water intakes, filters, control gates, etc.) so they can be operated efficiently even if zebra mussels become established, or readily adapted to do so.

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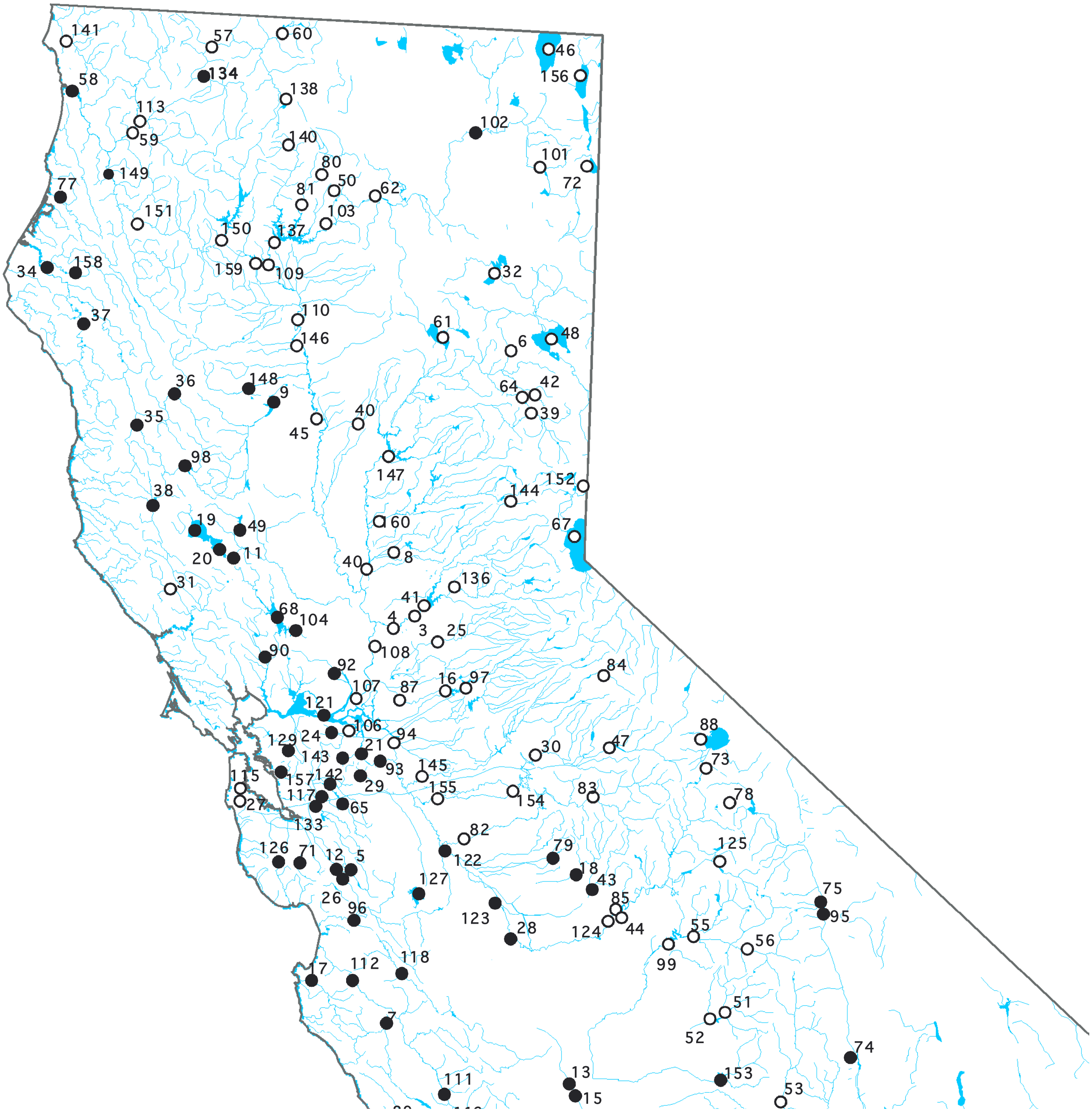
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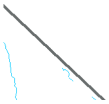

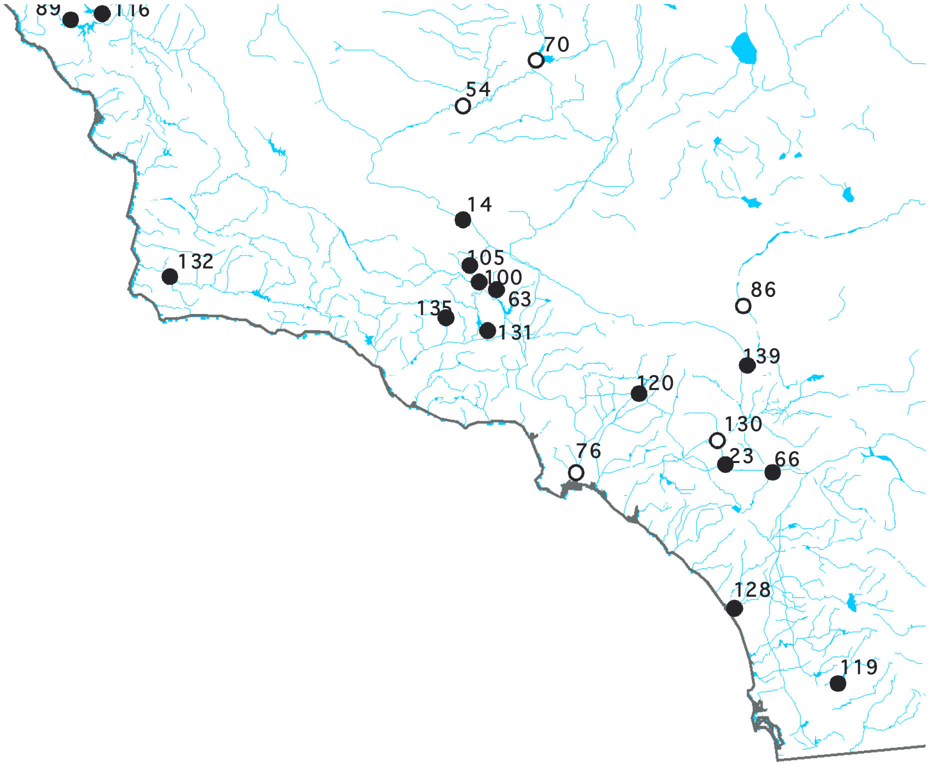
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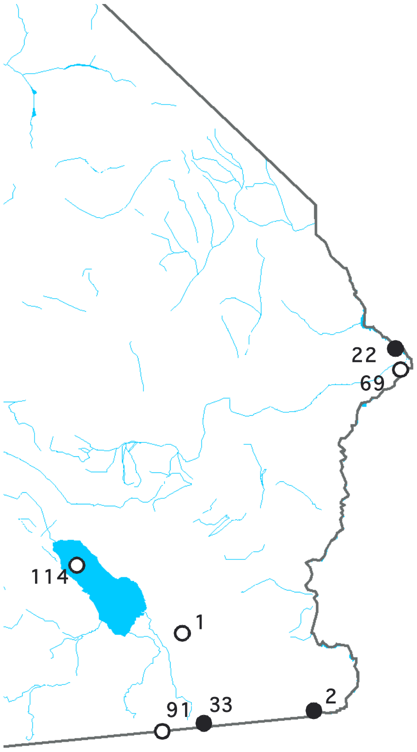
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