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Experimental Repatriation of Mountain Yellow-legged Frogs (*Rana muscosa*) in the Sierra Nevada of California

By Gary M. Fellers, David F. Bradford, David Pratt, and Leslie Wood

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Abstract

In the late 1970s, *Rana muscosa* (mountain yellow-legged frog) was common in the Tableland area of Sequoia National Park, California where it was possible to find hundreds of tadpoles and adults around many of the ponds and lakes. Surveys in 1993-1995 demonstrated that *R. muscosa* was absent from more than half of all suitable habitat within the park, including the Tableland area. At that same time, *R. muscosa* was still common at Sixty Lake Basin, Kings Canyon National Park, 30 km to the northeast. To evaluate the potential causes for the extirpation, we repatriated *R. muscosa* eggs, tadpoles, subadults, and adult frogs from Sixty Lake Basin to four sites in the Tableland area in 1994 and 1995. We subsequently surveyed each release site and the surrounding area 2 - 3 times per week in 1994-1995, and intermittently in 1996-1997, to monitor the survival of all life history stages, and to detect dispersal of adults and subadults. We also monitored predation, water quality, weather, and water temperature.

Our techniques for capturing, holding, transporting, and releasing *R. muscosa* were refined during the study, and during 1995 resulted in high initial survival rates of all life history stages. Adult frogs were anaesthetized, weighed, measured, tagged, and held in plastic boxes with wet paper towels. Tadpoles were collected and held in fiberglass screen cages set in the water at the edge of a pond. This resulted in relatively natural conditions with less crowding and good water circulation. Frogs, tadpoles, and eggs were placed in Ziploc bags for transport to the Tableland by helicopter. Short-term survival of tadpoles, subadults, and adults was high at all four release sites, tadpoles reached metamorphosis, and adult frogs were still present. However, we detected no evidence of reproduction at three sites (e.g., no new eggs or small tadpoles) and nearly all life history stages disappeared within 12 months. At the fourth site, there was limited reproduction, but it was insufficient to maintain a population.

It appears that the causal factors for the demise of *R. muscosa* in the Tableland during the 1970s were still operating in the 1990s or that a new limiting factor has developed. Dispersal, weather, water quality, and predation do not appear to be causative agents; since fish have never been present in the portions of the watershed where we were working, they were not a factor. Observations and data are consistent with the hypotheses that chytridiomycosis, caused by the chytrid fungus *Batrachochytrium dendrobatidis*, and/or exposure to airborne pesticides caused both declines. However, at the time of our study, chytridiomycosis had not been described and the potentially significant role of contaminants was largely undocumented.

Amphibians are declining in many areas around the world (Lips, 1999; Houlahan et al., 2000; Stuart et al., 2004). In the western United States, declines of frog, toad, and salamander populations have been widely reported and populations of several species appear to have been extirpated (Fellers and Drost, 1993; Drost and Fellers, 1996; Corn, 2000; Davidson et al., 2002). Healthy, seemingly well-protected populations have disappeared for no obvious reason. These losses are significant both because of the decline in biodiversity and also because amphibians are believed to be sensitive biological indicators of the health of the environment (Blaustein and Wake, 1990).

The causes of amphibian population declines are largely unknown, but several human and natural factors have been suggested, including land use changes, non-native predators and competitors, acidic waters, pesticides, long-term fire suppression, increased UV-B radiation, and disease (Hayes and Jennings, 1986; Bradford, 1989, 1991; Bradford et al., 1992, 1994b; Berger et al., 1998; Corn et al., 1989; Fellers and Drost, 1993; Lips, 1999; Fellers et al., 2001; Sparling et al., 2001; Stuart et al., 2004). Unfortunately, most of the declines have only been noted well after they occurred (but see Lips, 1999). One of the difficulties in identifying the cause(s) of declines is the lack of observations and/or experiments that coincided with the declines. In this study, we repatriated *R. muscosa* to the Tableland area so we could evaluate possible causes of decline.

Rana muscosa is one of the frogs that have declined dramatically in the western United States. It is currently a candidate for listing as an endangered species under the Endangered Species Act (USFWS, 2003), but the USFWS (2007) has determined that formal listing is "warranted but precluded." This frog was once abundant throughout much of the Sierra Nevada (Grinnell and Storer, 1924) and was common around mountain lakes, ponds, and meadow streams in the southern Sierra Nevada as recently as the 1970s (Bradford et al., 1994a). One of the authors (DB) conducted extensive field work on *R. muscosa* in Sequoia National Park from 1978 to 1980. At that time, it was possible to find hundreds of tadpoles and scores of adults around many of the ponds and lakes in the park (Bradford; 1983, 1991).

By the mid-1990s, *R. muscosa* populations had exhibited conspicuous declines throughout the southern Sierra Nevada. Surveys of 670 sites in Sequoia and Kings Canyon National Parks from 1993 to 1995 indicated that *R. muscosa* was apparently gone from more than half of suitable habitat (Fellers, unpub. data), including the study sites where the species was abundant in the late 1970s (Bradford et al., 1994a). There were, however, some areas where *R. muscosa* was still common, most notably at Sixty Lake Basin in Kings Canyon National Park, where large populations were present throughout our study (1993-1995; Fellers, unpub. data).

Land managers are increasingly interested in repatriations as a tool for preserving amphibian populations. Unfortunately, there are almost no useful data to guide decisions with respect to repatriations of declining amphibians, e.g., how to carry them out, how refugia can be established and protected, and how to mitigate causative factors (see review by Lind, 2004).

Dodd and Siegel (1991) and Dodd (2005) point out that programs to reestablish amphibian populations are often flawed by not investigating the causes for the original decline or extirpation. We designed our study to address this concern. Specifically, we wanted to evaluate the factors that might contribute to the decline of *R. muscosa*. Our goal was not to reestablish a viable population of *R. muscosa*. We expected that whatever caused the original loss would still be present, and that the repatriated frogs would likely decline. We conducted this study to recreate the conditions surrounding the loss of *R. muscosa* so we could evaluate causes of decline. We gathered data on growth, survival, dispersal, weather, water quality, predation, and contaminants along with data on survival of all life history stages, and reproductive effort (e.g. presence of new egg masses). Unlike most areas within the range of *R. muscosa* in the Sierra Nevada, the repatriation site never had fish in the upper portions of the watershed where our study took place, so fish were not a factor.

Unfortunately, our study was carried out several years prior to the description of chytridiomycosis in amphibians (Berger et al. 1998), and before pesticide drift from the Central Valley of California had been recognized as a potentially significant problem for Sierra Nevada amphibians (Sparling et al., 2001), so we never examined frogs or tadpoles for chytridiomycosis and only looked at pesticides as the repatriated frogs were dying off (Fellers et al., 2004).

METHODS

Study Animal

Rana muscosa breeds in high mountain ponds, lakes, and some streams in the Sierra Nevada at elevations from approximately 1500 - 3700 m (Zweifel, 1955). Eggs are laid immediately after snowmelt and tadpoles typically do not metamorphose until their third summer (Vredenburg et al., 2005). During mid-summer, nominal tadpole age classes are readily distinguished. First-year tadpoles are relatively small (< 40 mm total length), second-year tadpoles are appreciably larger with minute hind limbs (Gosner stage < 36; Gosner, 1960), and third-year tadpoles have conspicuous hind limbs (Gosner stage > 36). Adults probably mature and begin breeding after three or four years (Vredenburg at al., 2005). At our study areas, male *R. muscosa* develop secondary sexual characteristics when they reach approximately 4.5 cm snout-vent length, and weigh about 10 g. We refer to frogs > 4.5 cm as adults, and frogs less than that size as subadults.

Tableland Release Sites

We selected the Tableland area of Sequoia National Park (36° 37’ 05” N; 118° 38’ 16” W; Fig. 1) because of 1) the absence of *R. muscosa* in 1993; 2) the existence of several, large populations of *R. muscosa* within the previous 20 years; 3) availability of historic data on population size; 4) lack of non-native predators (e.g., trout); and 5) isolation from any extant populations of *R. muscosa* that could disperse into the study area.

During the 1970s, the Tableland area supported many hundreds of adult and larval *R. muscosa* at a minimum of 17 sites within a 15 km^2 area (Bradford, 1991; Bradford et al., 1994a). Population declines were first noted in the late 1970s (Table 1), and the last *R. muscosa* was seen in the Tableland area during an extensive survey there in 1989 (Bradford et al., 1994b). In 1993, Bradford and Fellers spent a week surveying all suitable frog habitat within the Tableland and found no *R. muscosa*, either in that watershed or in the upper reaches of the adjacent watersheds. Since it is relatively easy to detect adults and tadpoles in the clear, nearly vegetation-free ponds and lakes of the high Sierra, it is unlikely that we overlooked extant populations during repeated surveys prior to the experimental repatriation.

Unlike many places in the Sierra Nevada, the Tableland area was largely devoid of fish. Introduced fish were present in two nearby lakes (Moose Lake and Pear Lake), but only one lake upstream from these lakes or upstream from streams draining these lakes has ever had fish (1.0 km from Far Pond). Hence, fish did not appear to play a role in the decline of *R. muscosa* in the Tableland area, and fish were not a complicating factor for our study.

Migration of *R. muscosa* to and from the Tableland area during our study was unlikely. Non-native, predaceous trout inhabited all the streams in surrounding watersheds and at lower elevations in the Tableland watershed. Thus the streams could not easily serve as recolonization or dispersal corridors for *R. muscosa*. Non-native trout are known to eliminate *R. muscosa* populations where the two occur together (Bradford, 1989; Knapp and Matthews, 2000), and fish feed on both larvae (pers. obs.) and adults (Needham and Vestal, 1939). The nearest known *R.*

muscosa population was more than 10 km away, much greater than the 1 km that *R. muscosa* occasionally move (Vredenburg et al., 2005).

Rana muscosa were released at four sites (Fig. 1). Table Meadow is a 4.5 ha meadow (3,110 m elevation) with a stream running through it. Frog Lake is a small lake (2 ha, 4.1 m maximum depth, 3,080 m) that lies 250 m southwest of Table Meadow. In the late 1970s, it supported a large population of *R. muscosa*. Far Pond (1 ha, 2.7 m maximum depth, 3,290 m) is one of a chain of ponds at the head of a small drainage. Full Moon Pond (1 ha, 2.6 m maximum depth, 3,230 m) is also at the head of a small drainage. *Rana muscosa* populations existed at all four of these sites in the late 1970s. Frog Lake and Far Pond were referred to as sites G-013 and G-049 by Fellers et al. (2004). The third pond downstream from Far Pond was referred to as G-054 by these authors, whereas we have designated it Dispersal Pond 3.

Sixty Lake Basin Donor Area

Criteria for selecting the donor area were 1) a large population of apparently healthy *R. muscosa*; 2) elevation within 150 m (500 ft) of the release sites; 3) proximity to the Tableland area; and 4) a genetically diverse group of donor populations. Sixty Lake Basin in Kings Canyon National Park (36° 48’ 35” N; 118° 25’ 29” W) was selected as the donor area. The basin was one of the closest areas to the release sites (30 km) that still supported substantial populations of *R. muscosa*. During 1993-1994 surveys, we found 1,718 adult frogs, 1,289 subadults, and 16,027 larvae at 65 sites within the basin. We limited the impact on donor populations by collecting only from the largest populations, and by not removing more than 20% of any life history stage, i.e. egg, tadpole, subadult, or adult. Typically, the removal was < 5% of any one stage. The donor site elevations (3,250 - 3,345 m; 10,660 - 10,975 ft) were similar to that of the Tableland release sites [3,080 - 3,290 m (10,105 - 10,794 ft)]. The area had also been identified as having one of the most genetically diverse populations of *R. muscosa* in the southern Sierra Nevada, based on mitochondrial DNA analysis (H. Bradley Shaffer and Gary M. Fellers, unpub. data).

Life History Stages and Definitions

Rana muscosa breed in high mountain ponds, lakes, and occasionally streams in the Sierra Nevada at elevations from approximately 1,500 - 3,700 m (4,900 - 12,150 ft) (Zweifel, 1955). Eggs are laid immediately upon snowmelt, sometimes while there is still ice around the edges of ponds. Tadpoles typically metamorphose during their third summer. At the highest elevations, it may take four summers (Vredenburg at al., 2005), and at the lowest elevations, tadpoles metamorphose after only one summer (Storer, 1925). During mid-summer, nominal age classes are readily distinguishable.

Capture, Handling, and Transportation

1994

On June 11 - 14, eight egg masses, 468 second-year tadpoles, 624 third-year tadpoles, and 97 subadult frogs were collected from nine ponds at Sixty Lake Basin. The number of tadpoles subsequently released was almost 40% lower due to mortality during the 1- 3 day holding period. We did not segregate frogs and tadpoles based on where they were collected. Subadult frogs were placed in plastic boxes (Rubbermaid, Wooster, OH; 29 x 18 x 7 cm) with six, 5.0 mm holes drilled in the lids to allow air circulation. Frogs (four per container) were kept moist with wet paper towels, which were changed once or twice a day as they became soiled. Eggs and tadpoles were held in 4 L plastic freezer bags (Ziploc, Racine, WI) that were not sealed shut. Bags were held upright by placing them (in sets of four) in 40 x 28 x 23 cm plastic containers without lids. Tadpole densities were approximately 25 per bag. Each egg mass was placed in its own bag. Water was changed every 1 - 2 hrs throughout the day and 3 - 4 times during the night. On June 14, the Ziploc bags were closed and all life stages were flown to the release sites by helicopter.

On September 15 - 16, 50 adult frogs (25 males and 25 females) were collected from five ponds at Sixty Lake Basin. They were held as described above for subadults. On September 16, the frogs were backpacked 18 km (11 mi) to the nearest trailhead, and driven to the west side of the range, where each frog was anaesthetized with 0.02% benzocaine (Fellers and Freel, 1995), measured (snout-vent length), weighed (to nearest 0.1 g), and marked with a PIT tag. PIT tags were inserted under the skin just posterior to the skull. Once the tag was inserted, it was manipulated externally so it rested over the pelvic girdle. The frogs were then backpacked 13 km (8 mi) into the Tableland where they were released on September 20.

1995

On August 24 and 25, 93 adult frogs (46 males and 47 females), 286 second-year tadpoles, and 324 third-year tadpoles (but no eggs or subadults) were collected at Sixty Lake Basin. Adult frogs were anaesthetized, weighed, measured, PIT-tagged, and held in Rubbermaid boxes with wet paper towels using the same techniques as in 1994. Unlike 1994, tadpoles were collected and put into fiberglass screen cages set in the water at the edge of a pond. This resulted in relatively natural conditions with less crowding and better water circulation compared with 1994. On August 26, they were transferred to 4 L Ziploc bags for about 45 min during transport to the Tableland by helicopter.

Release of Repatriated *Rana muscosa* at the Tableland Sites

1994

All life history stages were released at the Tableland sites in 1994 (Table 2). The release procedure was designed to facilitate acclimation to the new environment. About 10% of the water was poured out of the container every 5-10 min, and a similar amount of fresh pond water was added back in so that eggs and tadpoles could adjust to differences in water temperature and chemistry. In 1994, amphibians at Table Meadow, Frog Lake, and Full Moon Pond were released after an hour into a 2 x 1.5 x 1 m (L x W x H) temporary holding cage made of fiberglass screen supported by PVC pipe. The fiberglass and pipe had been washed with Downy soap (Procter and Gamble, Cincinnati, OH) and thoroughly rinsed to remove any manufacturing residue. The release cage was set at the edge of the pond so that one end was almost submerged and the other end was resting on the shore. This provided conditions suitable for both the aquatic and terrestrial stages. A head of crushed lettuce was added to each cage as a food supplement, since the normal complement of algae and phytoplankton might not have been readily available inside the cages. After two days, the cages were opened and all amphibians were allowed to swim freely into the pond.

At Far Pond (3,290 m), the pond was still 80% frozen during the day, and both darkness and refreezing of the pond at dusk prevented use of a holding cage. It was necessary to break the ice and release the eggs, tadpoles and subadult frogs directly into the pond after an hour acclimation as described above.

1995

Second-year, third-year, and adult frogs were released at three of the four Tableland sites in 1995 (Table 3). As in 1994, frogs and tadpoles were held temporarily in fiberglass screen cages at the edge of the pond, but this time they were released into the pond after only a few hours.

Rana muscosa Monitoring

In both 1994 and 1995, *R. muscosa* at the Tableland release sites were monitored every 1- 3 days throughout the summer. In 1994, monitoring occurred from the initial release on 14 June, and continuing until the onset of heavy snowfall on September 27. In 1995, monitoring extended from the time that ice melted from the lowest elevation site (August 1) until October 20, when ice was forming nightly on the higher elevation ponds. The sites were also monitored at approximately monthly intervals during the ice-free summers of 1996 and 1997, and during a single visit in September 1998.

Monitoring consisted of counting all life history stages while 1) walking the perimeter of each pond and the length of each bank of Table Meadow stream during the day, and 2) sweeping a dip net through the rather limited vegetation in or near the water to make frogs and tadpoles move and become more conspicuous. After adult frogs were released at the Tableland sites (September 20, 1994), monitoring was extended to include connecting streams and ponds within several hundred meters of all four release sites to evaluate dispersal. In 1995, adult frogs were caught at two-week intervals, scanned for PIT tags, weighed, measured, and examined for signs of disease or injuries. Frogs were also captured and examined in a similar fashion during surveys in 1996 - 1998.

Predator Surveys

At least once each week during the 1994 and 1995 field seasons, we surveyed each of the release sites for potential *R. muscosa* predators; the behaviors of possible predators were recorded, e.g., foraging in the water, foraging on land, flying, swimming, resting, passing through, fleeing, drinking, bathing, or other. Western terrestrial garter snakes (*Thamnophis elegans*) were captured when possible and palpated to determine if they had a food bolus. If a bolus was found, the snake was gently encouraged to regurgitate it so we could see whether the snake had fed on tadpoles, subadults, or adult frogs of either *R. muscosa* or *Pseudacris regilla* (Pacific treefrog) (Filippi et al., 2005). Garter snakes captured after mid-July 1994 were marked by clipping ventral scales with fine-tipped scissors. No other species of snake was seen during our study.

pH and Electrical Conductivity

At approximately one-week intervals throughout the summers of 1994 and 1995, we measured pH and electrical conductivity (EC) at all four release sites. The samples were collected from just below the water surface, using clean, rinsed, high-density polypropylene bottles. All samples were analyzed at our Tableland base camp, using battery-powered equipment. We calibrated the equipment prior to each use. The pH meter (Accumet, model 1001; Fisher Scientific, Los Angeles, CA) was calibrated with pH 4.0, 7.0, and 10.0 standards. The electrical conductivity meter (Hach Mini Conductivity Meter, model 17250; Hatch, Loveland, CO; www.hach.com) was calibrated with a 9.8 µS/cm standard.

Water Temperature

Water temperature was recorded hourly with data loggers (StowAway; Onset, Pocasset, MA). On August 5, 1994, two temperature loggers were deployed in Far Pond at depths of 0.5 and 1.0 m above the bottom, at a time when the water level was slightly more than a meter deep at that part of the pond. The data loggers were retrieved on August 23, 1995. The data loggers remained at 0.5 and 1.0 m above the bottom, but the water level in the pond had increased by about one meter.

From September 26, 1995 to August 21, 1996, we monitored water temperature at Full Moon Pond, Frog Lake, and Far Pond. At each pond, a pair of temperature loggers was deployed. One logger was weighted and lowered to the bottom in the deepest part of the pond. The other logger floated on the surface, connected by a nylon cord. The cord served to anchor the surface logger and to facilitate retrieval of the bottom logger.

Weather Data

Long-term weather data were obtained from the National Weather Service weather station at Grant Grove, California (36° 44' 21" N; 118° 57' 51" W), 32 km NW of the Tableland at an elevation of 1990 m (6,530 ft). This was the closest weather station with relatively complete long-term weather data. Data have been collected since November 1, 1940 and were obtained from the National Climatic Data Center (www.ncdc.noaa.gov).

Pesticides

On August 18 - 20, 1997, we were able to find only 20 *R. muscosa* in the Tableland area. All 20 frogs were collected, including 12 adult males, three adult females, and five subadults. Sixteen of the frogs were collected at Far Pond. Two frogs were collected at Dispersal Pond 3 (Fig. 9), and one was collected at Frog Lake. Each frog was anaesthetized in a 0.02% solution of benzocaine (Fellers and Freel, 1995), weighed, measured, and frozen in liquid nitrogen.

On August 22, 1997, 20 *R. muscosa* from Sixty Lake Basin donor sites were collected (10 adult males, 5 adult females, and 5 subadults) and similarly processed. Frogs came from two unnamed ponds described in Fellers et al. (2004). Frog samples were shipped on dry ice to the University of Nevada (Reno, NV) for processing. Tissue samples were analyzed for organophosphate insecticides, endosulfans, chlordanes, hexachlorocyclohexanes, and DDTs at the U.S. Department of Agriculture in Beltsville (MD). Methodological details are provided by Fellers et al. (2004).

At two ponds in the Tableland and two in Sixty Lake Basin, concurrent 4-liter water samples were also collected. Water was filtered through a glass fiber filter and extracted using a 4-g C18 solid-phase extraction cartridge [see LeNoir et al. (1999) for detailed description of the sample collection, processing, and analysis methods]. Water samples were analyzed for trifluralin, chlorpyrifos, chlorpyrifos oxon, chlorothalonil, endosulfan I and II, malathion, and diazinon. A detailed description of the sample collection, processing, and analytical methods has been published by LeNoir et al. (1999).

Statistical Analysis

Data were analyzed using Statistix (version 8.0, Analytical Software, Tallahassee, FL, USA). Mann-Whitney and Wilcoxon paired sample non-parametric tests were used because our data were not normally distributed. We used $P = 0.05$ to evaluate statistical significance. Measures of variability are given as standard deviations.

RESULTS

Eight egg masses, 1264 tadpoles, 97 subadults, and 143 adult frogs were released at the Tableland (Tables 2 - 3).

Survival during Collection, Holding, Transport, and Release

Eggs

All eight egg masses appeared to survive in good condition from time of collection until they were released. After release, some masses drifted from their original positions because they were not attached to vegetation, as they normally would be. A substantial buildup of pine pollen along the edge of the release ponds made it difficult to relocate egg masses. In spite of careful searches, we were unable to find two of the eight egg masses after one day, and could not find any of the egg masses after five days, hence we could not evaluate whether the eggs hatched.

Tadpoles

In 1994 there was almost 40% loss of tadpoles while holding them in Ziploc bags at Sixty Lake Basin prior to repatriation, probably due to crowding and/or lack of oxygen. The loss was primarily at night when the water was changed less frequently. Losses were greater for third-year than second-year tadpoles. In 1995, we used fiberglass screen holding cages placed at the edge of a pond, and tadpole survival was 100%. Survival of tadpoles during transport and release was >99% in both 1994 and 1995.

Subadults

There was no subadult mortality during collecting, holding, or transport. Three subadults were lost, however, during the release at Far Pond. That release was carried out in the dark when the pond surface was refreezing. One subadult was stepped on, another was found frozen in the snow the next morning, and the third was found dead underwater two days later. These problems were largely caused by late arrival of the transport helicopter, resulting in the release taking place at dusk, much later in the day than planned.

Adults

There was no mortality among the adult frogs repatriated from Sixty Lake Basin to the Tableland in either 1994, when they were transported overland for four days, or in 1995 when they were transported by helicopter.

Long-Term Survival of Tadpoles and Subadults

1994

We conducted more than 30 surveys at each of the four Tableland sites in 1994 (Fig. 2 - 5). Several patterns were evident at all four sites. 1) Counts for all life stages varied considerably among surveys, even for surveys within a few days of each other. Some, but not all, of the low counts were on days with adverse weather, e.g., low air temperature, strong winds, or rain. 2) The number of subadults in late summer exceeded the number released in June, demonstrating that some tadpoles successfully metamorphosed. 3) The number of tadpoles counted during early summer was usually well below the number actually present as shown by the number of subadults observed at the end of the season. Only a fraction of the repatriated tadpoles were observed at any one time, even within a few days of release. 4) Because tadpole counts were so low, it is not possible to determine if second-year tadpoles survived to their third summer. 5) Counts for both second- and third-year tadpoles declined to zero or very low numbers by late summer. 6) Tadpole and subadult counts were lowest at the Table Meadow site, where vegetation (especially willows, *Salix* sp.) hindered surveys. For this reason, subsequent releases were not done at Table Meadow.

1995

We conducted nine surveys at Table Meadow between August 1 and October 17, 1995, but no frogs, tadpoles, or eggs were found. We conducted 17 - 20 surveys at the three Tableland sites where tadpoles and adult frogs (i.e. no eggs, no subadults) were released in August 1995 (Fig. 6 - 8). As in 1994, the survey counts were highly variable. Counts of subadults (which were released only in 1994) were substantially lower in 1995 than in 1994 at both Full Moon Pond (1994: median = 15, n = 32 counts versus 1995: median = 1.5, n = 20) and Frog Lake (1994: median =10, n = 32 versus 1995: median = 0, n = 17), but were similar between years at Far Pond (1994: median = 34.5, n = 20 counts versus 1995: median = 22, n = 37). The absence of subadults at Full Moon Pond and Frog Lake during the early part of the 1995 season, and low numbers of subadults later in the season, suggest that subadults did not survive from 1994 to 1995. In contrast, many of the subadults at Far Pond survived the winter of 1994-1995. Tadpole counts were zero or near zero at all three sites at the beginning of the 1995 season, consistent with counts at the end of the 1994 season. First-year tadpoles were observed at only Far Pond. Three were found on 3 October, and four on 10 October. These tadpoles came from eggs oviposited at Far Pond in 1995.

1996-1998 Surveys for Tadpoles and Subadults

During 1996-1998, *R. muscosa* tadpoles were found at all three Tableland pond sites. Nearly all of these were third-year tadpoles (Table 4 - 6). The maximum counts in 1996 were substantially greater than counts at the end of 1995 (Fig. 6 - 8). The increase in tadpoles may have occurred in 1995 as well, but it would have been masked by the repatriation of additional tadpoles in 1995.

No subadults were found at Full Moon Pond or Frog Lake in July 1996, suggesting that none survived from 1995 (Tables 5 - 6, Fig. 5). At Far Pond, the low subadult numbers in July 1996 (compared to the number counted at the end of 1995) suggest that mortality was also high during the winter of 1995-1996 (Table 4, Fig. 6). Subsequent declines of second-year tadpoles, third-year tadpoles, and subadults at Far Pond during 1996-1998 indicate a loss due to metamorphosis and/or mortality, and little recruitment. The only documentation of reproduction during 1996-1998 was a single second-year tadpole found in Dispersal Pond 3 (Table 4, Fig. 9) in 1998, three years after the last second-year tadpole had been released.

Long-Term Survival of Adults

Frogs released in 1994

At both Far Pond and Full Moon Pond, frog numbers rapidly declined to 2/3 of the number released (Table 7). By 1995, frog counts at the two ponds differed from each other greatly. At Full Moon Pond, none of the 25 repatriated frogs was ever seen after 1994.

At Far Pond, 15 of the 25 frogs released in 1994 were captured in 1995, seven of the original 25 in 1996, and three in 1997.

Frogs released in 1995

At Far Pond, all 31 of the adults were captured at least once during the 1995 season; 15 were captured again in 1996, and two in 1997 (Table 8). At the other two sites, fewer frogs were captured in 1995 than at Far Pond, and only two of the repatriated frogs were found after 1995, both at Full Moon Pond at the start of 1996.

Recruitment of Adult *Rana muscosa* at the Tableland

Recruitment of adults from eggs, tadpoles, or subadults occurred only at Far Pond (Tables 4 - 6) as shown by the presence of adult frogs lacking PIT tags. After 1995, we found only three of the repatriated adult frogs, one at Frog Lake, and two at Full Moon Pond. In contrast, untagged adult *R. muscosa* were found at Far Pond in both 1996 and 1997. We tagged a total of 28 frogs there, 14 adults and 4 subadults in 1996, and 10 adults in 1997. Some of the adult frogs found at Far Pond in 1996 and in 1997 were not captured (Table 4). Since none of the unmarked adults was found until 1996, it seems likely that they developed from tadpoles released at Far Pond, rather than from the 25 (untagged) subadults released there in June 1994.

On July 15 - 17, 1997, all the frogs that we found appeared sick; two were found dead and three died within a day of being captured (Table 4). On August 19, 1997, all 20 frogs observed at our repatriation sites (15 adults, 5 subadults; 19 at or near Far Pond and one at Frog Lake) were collected for analysis of pesticides. Only one frog was observed during the 1998 survey. However, four adult frogs were found at Dispersal Pond 3 (near Far Pond, Fig. 9) in 2000, and one was found there in 2001 (Knapp, unpub. data).

Dispersal from Release Sites

All ponds and streams in the vicinity of the release sites were surveyed for frogs at the end of the 1994 field season, and at approximately two-week intervals throughout the 1995 field season. Far Pond was the site with the most suitable frog habitat in the immediate vicinity and we detected significantly more dispersal at Far Pond where 14 of the 56 released frogs (25%) were later found in nearby ponds, compared to 8 of 79 repatriated frogs (10%) at the other three sites combined (χ^2 = 6.54, P = 0.0106). No appreciable difference was found in the dispersal frequency of males and females; of the 22 dispersing frogs, 12 were females and 10 were males. Maximum straight-line dispersal distance ranged from 50 m to 510 m, with a median of 80 m (mean = 173 ± 138 SD).

Some frogs were detected at increasingly greater distances from their release site. Frog 7112 was released at Far Pond on 20 September 1994; it was found in Dispersal Pond 1 (25 m from Far Pond) on 21 September 1995, and was found in Dispersal Pond 3 (90 m from Far Pond) on 3 October 1996 (Fig. 9). Frog 6744 was released on 20 September 1994; it was found in Dispersal Pond 5 on 5 September 1995 and 10 October 1995, and in Dispersal Pond 6 on 19 October 1995 (Fig. 9). The total distance from Far Pond to Dispersal Pond 6 (via the connecting stream) was ≥ 800 m.

Frog 7026 dispersed away from the release site and then returned. On 26 August 1995, frog 7026 was released at Frog Lake; on 21 September 1995, it was > 200 m away in the stream flowing through Table Meadow (Fig. 10); on 5 October 1995, it was back in Frog Lake.

Not all dispersal was closely associated with water; in a few cases, the dispersal was across land. The route from Full Moon Pond to the two ponds to the north (Fig. 11) traverses a rocky slope and entailed a 30 m elevation gain over a distance of 500 m; at least 80% of the route was over land.

Growth of Adult Frogs

Adult frogs caught at Sixty Lake Basin donor area did not differ significantly in length between 1994 and 1995 [Snout-vent length (SVL) 5.6 vs. 5.5 cm], but they weighed significantly more in 1994 (18.5 vs. 14.7 g, Mann-Whitney U = 3545, $n = 143$, $P < 0.001$; Table 9). A comparison of weight/length^3 shows that the 1994 frogs had significantly (19%) higher values than 1995 frogs (U = 3970, $n = 143$, $P < 0.001$). At the Tableland release sites in 1995, almost all frogs gained weight after repatriation. Average weight gain at the three release sites ranged from 22 to 28%, with an average of 24% (Wilcoxon T = 1, $n = 47$, $P < 0.001$; Table 10). We recorded a similar, significant increase in length at all three sites combined (~2 mm; T = 32, $n = 47$, $P < 0.001$; Table 10). On 20 September 1995, the condition (weight/length^3) of repatriated frogs had significantly increased (by 19%) since their original capture on 25 August 1995 (0.095 g/cm^3 versus 0.085 g/cm^3; T = 84, $n = 47$, $P < 0.001$). Changes in weight for two representative frogs, one repatriated to the Tablelands in 1994 (Fig. 12), and the other in 1995 (Fig. 13), show summer weight gain and winter weight loss, a pattern that was similar to other repatriated adult frogs.

Predation

During 1994 and 1995, we recorded 168 occurrences of potential *R. muscosa* predators at the four Tableland release sites. These included 92 observations of Brewer's blackbirds (*Euphagus cyanocephalus*), 39 of western terrestrial garter snakes, 23 of people (who might catch frogs), and four or fewer observations of each of the following: ravens (*Corvus corax*), eared grebes (*Podiceps nigricollis*), American dippers (*Cinclus mexicanus*), American kestrels (*Falco sparverius*), black bears (*Ursus americanus*), coyotes (*Canis latrans*), and alligator lizards (*Elgaria* sp.). The blackbirds were typically in groups of 10 or fewer. They often foraged both on land and in the shallow water, but the prey appeared to be insects. Despite hours of observation, we never saw them eating anything as large as a tadpole.

Of the 32 captures of western terrestrial garter snakes, eight had recently eaten larval or subadult *R. muscosa* or *P. regilla* (Table 11). All 39 observations and all 32 captures of western terrestrial garter snakes were at the three Tableland sites where the repatriated *R. muscosa* disappeared most rapidly. None were at Far Pond, where *R. muscosa* persisted the longest. All but four of the garter snakes were observed in 1994.

Amongst the birds, only the Eared Grebe seemed to have the potential to have an impact on *R. muscosa* since that species has been reported to eat both tadpoles and small frogs (http://www.houghtonmifflinbooks.com/peterson/resources/identifications/eagr/index.shtml#feeding; http://sdakotabirds.com/species/eared_grebe_info.htm). In 1995, a single eared grebe was seen at Full Moon Pond during three consecutive surveys (September 27 and 28, and October 4). It had not been there during any of the earlier surveys, (September 21 or before), nor was it there on October 11 or any subsequent survey in 1995. When present, the grebe remained in the center of the pond, where the water depths were 1 - 2 m at the time. We observed it with binoculars from a distance of approximately 30 meters. The water was clear, so that it was easy to see the grebe underwater. It repeatedly dove and swam in a meandering path along the bottom, typically for about 15 seconds, before it returned to the surface. It dove most frequently where the bottom was silt-covered rather than bare rock. While underwater, the grebe appeared to be moving continually, not obviously stopping to catch anything. During the three days that we encountered the grebe, we observed approximately 60 dives during an hour of watching. We could not determine whether the grebe was feeding on tadpoles. We were certain that the grebe never went into the shallow water where the tadpoles were usually seen. Only once did the grebe appear to surface with something in its beak that might have been a frog or tadpole. On that occasion, the grebe dropped the object back into the water and did not pursue it.

During and after the time the grebe was observed at Full Moon Pond in 1995, the counts of tadpoles, subadults, and adult frogs dropped to low levels and remained low (Fig. 7). Whether this was due to predation by the grebe was unclear since it could also have been due to reduced activity with the onset of cold weather in the fall. During a September 19, 1998 survey of Full Moon Pond, there was an eared grebe present, yet we found no *R. muscosa*.

Water Temperature

By early January 1995, water temperature at the Far Pond shallow data logger (1.0 m above the bottom) had cooled to a constant 0° C, indicating freezing to that depth (Fig. 14). By mid-January, the deep data logger (0.5 m above the bottom) had also cooled to a constant 0° C. Both remained at zero until the unusually late thaw that began in August 1995. Unfortunately, since the data loggers were neither at the surface nor at the bottom of the deepest part of the pond, it was not possible determine when the surface froze or whether the pond froze to the bottom at its deepest point.

Surface temperatures during the 1995-1996 winter at Far Pond, Full Moon Pond, and Frog Lake indicate that the ponds froze over between late-November and early-December, and remained frozen until late June to early July 1996 (Fig. 15 - 17). Data from the bottom data loggers showed that none of the three ponds froze to the bottom at their deepest points during that winter. The two shallower ponds (Full Moon Pond and Far Pond) cooled to less than 4° C.

pH and Electrical Conductivity

During 1994, pH varied little from week to week; most values were between 6.0 and 7.0 (mean = 6.5 ± 0.4, range 5.7 - 7.8, n = 59; Fig. 18). We observed no seasonal trend (linear regression, $R^2 = 0.0074$, T = 1.15, $P = 0.25$). In 1995, pH ranged from 6.02 to 7.01 (mean = 6.5 ± 0.3, n = 34; Fig. 19), and showed a slight rise through the summer. Conductivity (an indication of the quantity of dissolved electrolytes) was mostly between 2 and 10 µS/cm (mean = 5.2 ± 4.5, range 1.5 - 32, n = 93). Conductivity was significantly lower in 1995, a year of high precipitation (98 cm above normal), than in 1994, a year of low precipitation (34 cm below normal; National Weather Service, Grant Grove, CA) (T = 5.53, $P < 0.001$, n = 93).

Conductivity values were lower in Far Pond and Full Moon Pond, at the tops of their watersheds (mean = 3.0, n = 46), than they were in Frog Lake and the Table Meadow stream (mean = 7.3, n = 47), farther down in their watersheds in 1994 - 95 (T = 6.6, $P < 0.001$; Fig. 20 - 21). Values increased during each summer as snowmelt runoff decreased. The highest values were found in the Table Meadow stream late in the 1994 season, when stream flow had almost stopped.

Our measurements of electrical conductivity agree well with the observations of other researchers working a few kilometers downstream of our study sites, as well as measurements from elsewhere in the Sierra Nevada (Jim Sickman, *pers. comm.*). Electrical conductivity at the Marble Fork station in Sequoia National Park (downstream from three of the four Tableland sites) ranges from about 3 to 50 µS/cm. Sickman's data also demonstrate that larger snow packs lead to greater dilution, and lower electrical conductivity.

Pesticides

Analysis of the frog tissues showed that dichlorodiphenyldichloroethylene (DDE) concentrations were 1 to 2 orders of magnitude higher than the other organochlorine compounds, and DDE concentrations for Tableland frogs were significantly higher than those for Sixty Lake Basin frogs (46 ± 20 ng/g wet wt at Tableland area, 17 ± 8 ng/g at Sixty Lake Basin; Table 12). Concentrations of γ-chlordane and trans-nonachlor were also significantly greater in Tableland frog tissues compared with Sixty Lake Basin. The organophosphate insecticides, chlorpyrifos, and diazinon, were observed primarily in surface water samples, with higher concentrations at the Tableland sites (Table 13). No contaminants were found at significantly higher concentrations in our Sixty Lakes samples. Further results and details are presented in LeNoir et al. (1999) and Fellers et al. (2004).

DISCUSSION

Repatriation Techniques

Collecting all life history stages of *R. muscosa* was not difficult, in part because *R. muscosa* were abundant at Sixty Lake Basin donor sites during our study. Holding *R. muscosa* prior to repatriation to the Tableland was a problem only for tadpoles (primarily third-year tadpoles) in 1994. In 1995, we reduced tadpole mortality from 40% to zero by using screen holding cages placed at the edge of a pond. These cages allowed for the constant exchange of water, and tadpoles survived without mortality for up to two days.

In both years that we repatriated tadpoles, we did so by helicopter. This was necessary for two reasons. First, the water required to hold the tadpoles weighed approximately 115 kg (254 lbs). Second, our experience in 1994 indicated that mortality was unacceptably high when tadpoles were kept in plastic bags for an extended period. By contrast, we successfully moved 50 adult *R. muscosa* by backpack, then by vehicle, then again by backpack, over a four-day period. Tadpoles (especially third-year tadpoles) clearly represent the greatest challenge for repatriating *R. muscosa* in remote backcountry locations, but our use of mesh cages in 1995 showed that it could be accomplished with little or no mortality.

Release of tadpoles, subadults, and adults in the Tableland area was completed with almost no mortality. It appears that the cages used at the release site might not have been necessary; however, moving amphibians between less similar sites might warrant this approach. It is difficult to judge whether the slow addition of water into the plastic bags used for transporting eggs and tadpoles was important, but we recommend it as a standard procedure that allows for a slow adjustment to differences in temperature and water chemistry.

Our technique for repatriating *R. muscosa* eggs did not work well. Whether the eggs were eaten by predators, or survived and hatched, they all disappeared within a week. We recommend that repatriated eggs be placed in small fiberglass screen cages similar to those we used for holding tadpoles. This would keep the eggs in place until hatching, and allow for a more accurate assessment of short- and long-term survival of both eggs and early stage tadpoles.

Survival of Repatriated *Rana muscosa*

Both frogs and tadpoles repatriated to the Tableland area appeared to grow and develop normally. Adult *R. muscosa* at the release sites showed substantial weight gains and small increases in length during the summer of 1995. In 1994, the PIT-tagged frogs were not recaptured and reweighed, as the field season was terminated by a heavy snow that fell only a few days after the frogs were released at the Tableland area. Weight loss during the winter presumably occurred due to loss of fat reserves. By late summer of 1995, frogs reached a weight/length^3 ratio similar to that measured late in the previous summer when they were first captured at the donor sites. This strongly suggests that frogs released in the Tableland area were able to obtain sufficient food, and grow at a normal rate. At three ponds in 1994, and at Far Pond in 1995, metamorphosis of tadpoles occurred since the maximum number of subadults substantially exceeded the number repatriated at the start of the season. Metamorphosis continued into 1996, particularly at Far Pond. These observations indicate that survival and successful development of third-year tadpoles occurred through metamorphosis.

In spite of the growth of adults and development of tadpoles, long-term survival of *R. muscosa* was poor, and there was only limited reproduction. There was a clear downward trend in our counts in 1994-1998, despite variation between surveys. While the number of subadults increased initially in 1994 and 1995 as a result of metamorphosis, the number of subadult frogs declined by the end of each year. With the exception of Far Pond, there was almost no survival of subadults through the winter. Adult survival was also poor; adults disappeared precipitously at Full Moon Pond and Frog Lake, and more slowly at Far Pond.

Tadpole counts for both second- and third-year individuals also declined rapidly, to nearly zero by the end of the summers of 1994 and 1995. These counts, however, were not indicative of the number present. Mid-season tadpole counts clearly underestimated the number present, as shown by the number of subadults appearing later in the season. The extremely low tadpole counts at the end of the season were also a poor reflection of actual numbers, at least in 1995, because third-year tadpoles became evident in mid-summer of 1996, a year when no new tadpoles were repatriated to the sites.

Reproduction was extremely limited. Though we regularly found large numbers of egg masses at Sixty Lake Basin donor sites during surveys in 1994 and 1995, we never saw egg masses in the Tableland area. The only evidence of reproduction at the Tableland sites was in or near Far Pond, where we found a few first-year tadpoles in 1995, and a single second-year tadpole in 1998, three years after the last second-year tadpole had been released. These findings indicate that there was some reproduction in the Tableland area, but it was insufficient to maintain the population.

The lack of significant survival or reproduction strongly suggests that the Tableland sites were not suitable for *R. muscosa*. Whatever caused the disappearance of *R. muscosa* from the Tableland during the late 1970s and 1980s still appears to have been inhibiting the survival of *R. muscosa* 10 - 15 years later. Other studies have shown that repatriations of *R. muscosa* can be successful if the factor causing the original decline has been eliminated. For example, in August 2001, Roland Knapp (*pers. comm.*) repatriated 10 adult *R. muscosa* and 200 tadpoles into a lake in the Humphrey's Basin in the Sierra Nevada where introduced trout had been removed. By late 2002, the frog population consisted of approximately 100 adults and 300 first year tadpoles. This demonstrates that the relatively small number of adults used in the initial introduction was sufficient to allow reproduction and survival. Unfortunately, the population was extirpated because of a die-off apparently caused by the chytrid fungus *Batrachochytrium dendrobatidis* (Knapp, *pers. comm*.). However, as Dodd and Seigel (1991) and Dodd (2005) point out, most attempts at repatriation do not result in sustainable populations.

Possible Causes for the Loss of *Rana muscosa*

Any explanation of the failure to reestablish *R. muscosa* in the Tableland area must account for both the conspicuous loss of adults and subadults, and the minimal amount of reproduction. Specifically, 1) All adults at Full Moon Pond disappeared during the winter of 1994-1995, and only two survived the winter of 1995-1996; 2) All adults at Frog Lake disappeared during the winter of 1995-1996 (they were not present in 1994); 3) Although adults at Far Pond survived both winters, few repatriated individuals survived until 1997, and relatively few of the frogs that metamorphosed at this site were found as adults in 1997; 4) Several adults at Far Pond in August 1997 were dead or dying, and many appeared sick; 5) Although many subadults at Far Pond survived the winter of 1994-1995, survivorship was poor at this site through the winter of 1995-1996. Data on dispersal, weather, water quality, predation, disappearance of individuals by life stage, and contaminants were used to evaluate potential causes of decline. Fortunately, our study site was in a fishless area, so the impact of non-native trout was not a factor as it is throughout most of the Sierra Nevada (Vredenburg, 2004).

Weather Patterns

The most conspicuous deviation from normal weather patterns during our study (1994-1997) was the winter of 1994-1995 (Fig. 22 - 23). October 1994 was colder than normal, and was followed by the coldest November in the more than 60 years that weather records have been kept (National Weather Service data, Grant Grove, CA). Beginning in January 1995, snowfall was much heavier than normal, delaying the summer thaw until the beginning of August 1995. Also, the preceding winter was drier and warmer than normal, so water levels were relatively low. These conditions were similar to the winter of 1977-1978, when adult *R. muscosa* did not survive the winter at many Tableland sites, including the three repatriation ponds in our study (Bradford, 1983). Those die-offs were attributed to winterkill due to oxygen depletion in the water, which is more pronounced in shallow lakes and ponds. Thus, the disappearance of both adults and subadults from Full Moon Pond and Frog Lake during the winter of 1994-1995 may have occurred for this reason. For Full Moon Pond, while there was no temperature data logger in the pond during the 1994-95 winter, the data logger at Far Pond showed that the pond was frozen to a depth of at least one meter, suggesting that the Full Moon Pond was probably frozen to or near to the bottom as well. Nevertheless, unusual temperatures and precipitation were not evident during the 1995-1996 winter, and thawing at the release sites occurred in late June to early July (Fig. 15 - 17). Consequently, winterkill due to oxygen depletion or freezing was not likely to be responsible for the loss of adults and subadults at these two sites during the 1995-1996 winter. Temperature profiles at both of these sites indicated that the water did not freeze to the bottom (Fig. 16 - 17). Moreover, this does not account for the much greater survivorship of these life stages at Far Pond (our highest elevation site) than the other two sites during the winters of both 1994-1995 and 1995-1996. Far Pond (2.7 m deep at high water) is shallower than Frog Lake (4.1 m at high water) and bottom temperature profiles during winter were more similar to Full Moon Pond than to Frog Lake (Fig. 15 - 17).

Water Quality

We measured pH and electrical conductivity (EC) to evaluate whether water quality played a role in the disappearance of *R. muscosa*. Lakes in the Sierra Nevada are typically low in acid-neutralizing capacity and are, therefore, susceptible to acidification (Melack et al., 1985; Landers et al., 1987). Sierran Lakes are also low in ionic strength (Landers et al., 1987) and low pH levels would be expected to cause the most physiological stress at low ionic strengths (Freda and Dunson, 1984). While the EC values we measured were low compared with other Sierran lakes (Eilers et al., 1987; Bradford et al., 1994b; Sickman, *pers. comm.*), it is unlikely that the EC and pH we observed would be deleterious to *R. muscosa*. In a study of amphibian habitats at high elevations throughout the Sierra Nevada, Bradford et al. (1994b) found no association between the presence/absence of *R. muscosa* at a site and the pH or EC of the water. Moreover, the pH and EC values observed by Bradford et al. at sites inhabited by *R. muscosa* (e.g., minimum pH = 5.6, minimum EC = 3 μS/cm) included or were close to the values observed in our study (minimum pH = 5.6, minimum EC = 2 μS/cm).

Predators

Predators may have been a minor contributing factor in the loss of *R. muscosa*. In 1994, western terrestrial garter snakes were common at Table Meadow, Frog Lake, and Full Moon Pond. Five of 32 garter snakes contained the remains of *R. muscosa*. This included 3 of 6 snakes captured at Frog Lake, 2 of 18 at Full Moon Pond, and 0 of 8 at Table Meadow. We never observed snakes at Far Pond, where *R. muscosa* survived much longer than at the other three sites. The lack of snakes at Far Pond might be because that pond was in a granite basin with little vegetation. However, the three sites that did support snakes had historically supported large populations of *R. muscosa*. Garter snakes occur throughout the range of *R. muscosa*, but they occur almost exclusively at sites where either *R. muscosa* or *P. regilla* are present (Jennings et al., 1992; Matthews et al., 2002). Thus, the presence of this native snake is unlikely to be the primary cause of the loss of *R. muscosa*, especially since snakes would be inactive during winter when many adult and subadults disappeared.

A single grebe was seen at two of the release sites, Full Moon Pond and Frog Lake. Even with careful, extended observations, we were unable to ascertain whether the grebe was eating *R. muscosa*. Regardless, it is unlikely that foraging by just one individual of this naturally occurring native predator would be the primary factor leading to the loss of frogs, particularly during the winter.

Dispersal

Of the 143 adult *R. muscosa* released at the Tableland sites, at least 22 (15.4%) dispersed to nearby ponds or streams. It would be useful to know whether the dispersing frogs were merely moving away from their release sites, or if they were heading in the direction of the donor ponds. Sixty Lake Basin donor sites were 30 km northeast of the Tableland. Twenty of the 22 dispersants moved north, and most went somewhat east of north. However, most of the dispersing frogs that we located were from Far Pond, and the only suitable frog habitat was downstream to the northeast (Fig. 9). Dispersal in any other direction would have led frogs to a steep talus slope where survival would have been unlikely, and where we would not have detected their presence.

Two of the four frogs that dispersed from Full Moon Pond almost certainly traveled overland, rather than following a drainage channel, and to the northeast. We found only one frog that metamorphosed at a Tableland site that left its pond. That frog left Dispersal Pond 3 (where it was tagged as an adult) and went south to Far Pond. Pope and Matthews (2001) reported that 17% of their 500 PIT-tagged *R. muscosa* in Kings Canyon National Park moved overland during 1997 and 1998, so this type of behavior has been documented in other nearby populations.

During an extensive survey of the Tableland area in 2000, only four frogs were found (at Dispersal Pond 3, approximately 200 m downstream from Far Pond; Knapp, *pers. comm*.). It seems unlikely that dispersal alone would account for the loss of frogs, particularly during winter. Matthews and Pope (1999) evaluated movement of 24 *R. muscosa* using radiotransmitters. They found that movement varied seasonally with the greatest movement occurring in September with a mean distance moved of 145 m during that month, and the least movement at the onset of winter dormancy during October (43 m). These distances are similar to what we observed in the

Tableland area, hence it does not seem that dispersal from the release sites is a likely cause of the loss of frogs, especially considering that frogs were getting sick and dying at the release sites.

Disease

Infection by the chytrid fungus *B. dendrobatidis* is a plausible cause for the loss of *R. muscosa* in the Tableland, both during the 1970s and 1980s, and during our experimental reintroduction in the 1990s. Prior to 1998, it was thought that chytrid fungi did not infect vertebrate hosts. In 1998, Berger et al. (1998) described chytrid infections in frogs. Several subsequent studies provided strong correlative evidence that *B. dendrobatidis* was involved with declines in frog populations in both Panama (Lips, 1999) and Australia (Berger et al., 1998). Fellers et al. (2001) reported *B. dendrobatidis* in *R. muscosa* from the Sierra Nevada, less than 150 km north of the Tableland area. Recently, Rachowicz et al. (2006) demonstrated through extensive field surveys and laboratory and field experiments that chytridiomycosis was the proximate cause of numerous observed *R. muscosa* population declines in the southern Sierra Nevada. A conspicuous finding was that post-metamorphic stages of *R. muscosa* experience high mortality from chytrid infection, whereas tadpoles do not. Tadpoles infected with *B. dendrobatidis* survive to metamorphosis, but typically succumb to chytrid infection shortly after metamorphosis. This pattern is consistent with the die-offs and disappearances of adults, subadults, and recently metamorphosed frogs that were observed in the Tableland in the 1970s (Bradford, 1983; 1991), as well as during the present study. Since chytrid infection of frogs was not described until after our study, we did not look for it during our experimental repatriation.

Bradford (1991) reported a massive die-off of *R. muscosa* in a Tableland population during the summer of 1979 that appeared to be caused by red-leg disease, an infection caused by the bacteria *Aeromonas hydrophila*. Carey et al. (1999) suggested that the 1979 die-off may have been caused by *B. dendrobatidis* and that the bacterial infections were secondary, a hypothesis that cannot be tested today. *Aeromonas* is unlikely to be involved with the loss of repatriated *R. muscosa* during our study since we found no evidence of this disease (reddening of the thighs) in any of the frogs we handled.

Viral infections have been reported in *Rana aurora* (Mao et al. 1999). Die-offs caused by ranavirus typically kill only tadpoles and recently metamorphed (30-60 days) individuals, and there are often hundreds of dead tadpoles present at a site. By contrast, chytridiomycosis affects only adult anurans, often with only one or a few dead individuals present at a site (D.E. Green, *pers. comm.*). The extent of viral infections in California amphibians is unknown, but a large die-off of *R. muscosa* tadpoles in Kings Canyon National Park in 2001 appears to have been caused by an iridovirus (Knapp, *pers. comm.*). The significance of viral infections in declining amphibian populations remains largely unknown, but it does not appear to have been a factor in our study since we never observed tadpole die-offs.

Pesticides

Exposure to airborne pesticides is a possible cause for the Tableland population declines. Davidson and Knapp (2007) evaluated over 6800 sites in the southern Sierra Nevada for the presence of *R. muscosa*, the presence of introduced game fishes, habitat conditions, and the predicted exposure to windborne pesticides applied in upwind agricultural areas. In multivariate analyses, predicted exposure to pesticides had a pronounced negative effect on *R. muscosa* site occupancy, independent of other factors. This pattern is corroborated by our comparison of frogs from sites in the Tableland (an area near the Central Valley that has high predicted pesticide exposure) and frogs from Sixty Lake Basin (an area more remote from the Central Valley that has low predicted pesticide exposure). When the survival of *R. muscosa* in the Tableland area seemed unlikely in 1997 and most of the remaining frogs appeared sick, the last 20 *R. muscosa* were collected so pesticide concentrations could be compared with a similar set of frogs collected at the Sixty Lake Basin donor sites. Several pesticides, especially pp-DDE, were found at higher concentrations in frog tissue from the Tableland sites (Fellers et al., 2004).

Based on traditional toxicological studies that expose animals to contaminants for only brief periods of time (24 - 96 hr), it seems unlikely that the loss of *R. muscosa* was caused by the relatively low concentration of pesticides that have been found in the Tableland area. However, Relyea and Mills (2001) showed that increasing contaminant exposure from four to 10 days caused a significant increase in mortality. Thus, some of the contaminants in the Tableland may be present in concentrations sufficiently high to account for the loss of frogs. This is especially true for *R. muscosa* since they typically require three years for tadpoles to metamorphose, and 3 - 4 years for frogs to reach sexual maturity (Vredenburg et al., 2005). This means that *R. muscosa* tadpoles are exposed to contaminants in the water for an usually long time, possibly allowing them to accumulate more contaminants and making them (or the subsequent adults) more vulnerable (Sparling et al., 2001). In addition, it has been suggested that pesticide exposure may affect amphibian populations by suppressing immune function, thus making amphibians more susceptible to disease (Davidson and Knapp, 2007).

Other Factors

Several additional factors seem unlikely to account for the failure to re-establish populations. Introduced fish have been shown to dramatically affect the distribution and abundance of *R. muscosa* populations (Bradford, 1989; Knapp and Matthews, 2000). However, the Tableland area is largely devoid of fish and none occurred within 1 km of the study sites. Fellers and Drost (1983) suggested that fire suppression contributed to the loss of *R. cascadae* in northern California, but the vegetation in the Tableland area is not sufficient to support fires. There is no evidence that poor nutrition was a contributing factor, given that adults grew at a normal rate and tadpoles successfully metamorphosed in several years. It is possible that larger numbers of repatriated individuals would have resulted in greater success, but the repatriation of similar numbers of individuals elsewhere resulted in successful re-establishment of a population (Knapp, unpub. data).

CONCLUSIONS

Our study demonstrated the practicality of repatriating *R. muscosa*. We tested a variety of techniques for holding and moving all life history stages, and found that most of our techniques were both practical and appropriate for moving frogs between field locations.

Frog populations did not become established after four years, even though tadpoles metamorphosed and adults increased in both weight and length. The mechanism for this failure appeared to be primarily loss of adults and subadults, and very little reproduction. We examined a number of factors that might have caused the declines, e.g., weather, water quality, predation, and dispersal. In addition, we evaluated the general health of repatriated frogs in terms of weight/length^3. None of these factors appeared to be the primary cause of the decline. Introduced fish were not involved due to their absence from our study area. Both pesticides and chytridiomycosis have the potential to have caused the observed declines, either individually or in combination with other stressors. Further research is needed to clarify the role of each stressor.

While we did not identify the specific cause for either the original or subsequent loss of *R. muscosa* in the Tableland area of the Sierra Nevada, the evidence is compatible with chytridiomycosis and contaminants as a primary cause of the decline. Either one of these factors, or the two acting in concert, may have made the Tableland area unsuitable for *R. muscosa*. Hopefully, ongoing research on *R. muscosa* and other anurans in the Sierra Nevada will help elucidate this situation and allow for reestablishment of viable *R. muscosa* populations.

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Table 1. Historic records of *Rana muscosa* at the four Tableland area release sites at Sequoia National Park, CA (Bradford, unpub. data). The absence or very low numbers of adult frogs in 1978 at Frog Lake, Far Pond, and Full Moon Pond represented a dramatic decline from the previous year (Bradford 1983).

Site	Life History Stage	1977	1978	1979	1980	1989	1993
Table	Adults + Subadults	52	65	54	5	7	0
Meadow	Tadpoles	present	hundreds	hundreds	15	14	0
Frog	Adults + Subadults	48 +	1	0	0	0	0
Lake	Tadpoles	present	130	0	0	0	0
Far	Adults + Subadults	not visited	0	not visited	not visited	0	0
Pond	Tadpoles	not visited	260	not visited	not visited	0	0
Full Moon	Adults + Subadults	33 +	0	0	1?	0	0
Pond	Tadpoles	not recorded	present	9	0	0	0

Table 2. *Rana muscosa* repatriated in 1994 from Sixty Lake Basin (Kings Canyon National Park) to the Tableland sites (Sequoia National Park, CA).

	June 14 - 16				Sept. 20
		2nd year	3rd year		
Release Site	**Egg Masses**	**Tadpoles**	**Tadpoles**	**Subadults**	**Adults**
Table Meadow	2	80	84	25	0
Frog Lake	2	80	84	24	0
Far Pond	2	80	84	25	25
Full Moon Pond	2	78	84	23	25
Totals	8	318	336	97	50

Table 3. *Rana muscosa* repatriated in 1995 from Sixty Lake Basin (Kings Canyon National Park) to the Tableland sites (Sequoia National Park, CA).

	August 26, 1995		
Release Site	2nd year Tadpoles	3rd year Tadpoles	Adults
Table Meadow	0	0	0
Frog Lake	96	108	31
Far Pond	94	108	31
Full Moon Pond	96	108	31
Totals	286	324	93

Table 4. Counts of *Rana muscosa* at Far Pond and adjacent dispersal ponds in 1996-1998.

	2nd Year Tadpoles	3rd Year Tadpoles	Subadults	Adults			
					Recruits[1]		
				Repatriated[2]	Previously Tagged	Not Previously Tagged	Not Captured[3]
7/10/96	0	0	2	2	0	3	3
7/12/96	0	0	5	9	0	2 + 1 dead	9
8/22/96	1	28	12 + 4* + 2 dead	6	0	9 + 14*	1
10/1/96	0	0	6	7	2	5	1
10/3/96	0	0	10	10	7	4	1
7/15/97	0	0	0	2	4 (1 died)	5*+1 dead	1
7/16/97	0	1	1	1	0	3* (2 died)	5
7/17/97	0	2	0	1	3	2*(1 died)	2
7/20/97	0	4	1	1	6	4	1
8/19/97	0	0	5	4	6	5 + 1 dead	0
9/19/98	1**	0	0	0	0	1	0

1. Recruits were adults without PIT tags when first captured at Far Pond in 1996-1998. Hence they developed into adults at Far Pond from tadpoles or subadults that had been repatriated in 1994 or 1995.

2. Repatriated frogs were captured at Sixty Lake Basin, PIT-tagged, and released at Far Pond in 1994 or 1995.

3. Not Captured frogs were adults seen but not caught, and hence not examined for PIT tags.

* Number of adults or subadults without PIT tags that were tagged on this day.

** Located at pond Dispersal Pond 3, downstream from Far Pond (Fig. 9).

Table 5. Counts of *Rana muscosa* at the Full Moon Pond release site in the Tableland area (Sequoia National Park) in 1996-1998. Definitions as in Table 4.

Date	2nd year Tadpoles	3rd year Tadpoles	Subadults	Adults	
				Repatriated	Recruits
7/10/1996	0	4	0	1	0
7/11/1996	0	0	0	1	0
8/23/1996	0	33	2	0	0
10/2/1996	0	0	0	0	0
7/21/1997	0	0	0	0	0
9/19/1998	0	0	0	0	0

Table 6. Counts of *Rana muscosa* at the Frog Lake release site in the Tableland area (Sequoia National Park) in 1996-1998. Definitions as in Table 4.

Date	**2nd year Tadpoles**	**3rd year Tadpoles**	**Subadults**	**Adults**	
				Repatriated	**Recruits**
7/10/1996	0	5	0	0	0
7/11/1996	0	12	0	0	0
8/23/1996	0	1	4	0	0
10/2/1996	0	0	0	0	0
10/3/1996	0	0	0	0	0
7/19/1997	0	1	1	0	0
8/20/1997	0	0	0	0	0
9/19/1998	0	0	0	0	0

Table 7. Survival of PIT-tagged adult *Rana muscosa* released in 1994 at Far Pond and Full Moon Pond. Dates of the first and last surveys in 1995 were August 23 and October 19; dates for 1996 and 1997 are provided in Tables 4 and 5.

	Far Pond	Full Moon Pond
Number Released	25	25
1994 Surveys*	18	19
1995 Surveys**		
First	15	0
Last	10	0
1996 Surveys**		
First	7	0
Last	5	0
1997 Surveys**		
First	3	0
Last	2	0

*Maximum number of individuals observed during any single survey.

** Maximum number of individuals known to be alive at the time of survey. The number of frogs captured during each survey was increased by the number of PIT-tagged individuals subsequently captured and hence known to be alive at the time of the survey.

Table 8. Survival of PIT-tagged adult *Rana muscosa* released in 1995 at three sites in the Tableland area. Dates of the first and last surveys in 1995 were August 27 and October 17 - 20, dates for 1996 and 1997 are provided in Tables 4 and 5.

	Far Pond	Full Moon Pond	Frog Lake
Number Released	31	31	31
1995 Surveys			
First	31	20	22
Last	21	5	11
1996 Surveys*			
First	15	2	0
Last	8	0	0
1997 Surveys*			
First	2	0	0
Last	2	0	0

* Maximum number of individuals known to be alive at the time of survey. The number of frogs captured during each survey was increased by the number of PIT-tagged individuals subsequently captured and hence known to be alive at the time of the survey.

Table 9. Weight and snout-vent length of *Rana muscosa* when first captured at Sixty Lake Basin (Kings Canyon National Park) donor site. The ratio represents weight/length^3.

Year	Number Repatriated	Average Weight (g)	Average Length (cm)	Ratio g/cm^3
1994	50	18.5	5.66	0.102
1995	93	14.7	5.54	0.086

Table 10. Adult *Rana muscosa* weight and snout-vent length (SVL) gains at each of the three Tableland release sites in 1995. Frogs were originally captured, tagged, weighed, and measured at Sixty Lake Basin on August 25, 1995, repatriated to the Tableland area the next day, and recaptured on September 20, 1995. Numbers are means ± one standard deviation.

		August 25, 1995		September 20, 1995		Gain	
Release Site	N	Weight (g)	SVL (cm)	Weight (g)	SVL (cm)	Weight (g)	SVL (cm)
Far Pond	24	13.84 ± 3.32	5.45 ± 0.46	16.70 ± 3.29	5.62 ± 0.48	2.86 ± 1.45	0.17 ± 0.22
Full Moon Pond	10	13.78 ± 4.04	5.37 ± 0.51	17.38 ± 4.32	5.52 ± 0.48	3.60 ± 0.51	0.16 ± 0.14
Frog Lake	13	14.19 ± 3.94	5.51 ± 0.61	17.34 ± 4.48	5.69 ± 0.56	3.15 ± 1.42	0.18 ± 0.17

Table 11. Number of western terrestrial garter snakes (*Thamnophis elegans*) observed, captured, and containing frog remains at the Tableland sites in 1994 and 1995. *Rana muscosa* and *Pseudacris regilla* are both frogs (mountain yellow-legged frog, Pacific treefrog).

	Number	**Number**	**Snake stomachs with**	
Site	**Observed**	**Captured**	***Rana muscosa***	***Pseudacris regilla***
Table Meadow	11	8	0	1
Frog Lake	6	6	3	0
Full Moon Pond	22	18	2	2
Far Pond	0	0	0	0
Totals	39*	32**	5	3

* Only four observations were 1995.

** At least 16 of the 32 captured were different individuals based on marked scutes.

Table 12. Concentration of pesticides (ng/g wet wt) in *Rana muscosa* tissue collected at the Tableland (Sequoia National Park, n = 20), and the Sixty Lakes Basin (Kings Canyon National Park, n = 20) California, USA, 18 - 22 August 1997 (from Fellers et al. 2004).

	α-HCH[a]	γ-HCH[a]	γ-chlordane	trans-nonachlor	α-endosulfan	p,p'-DDE[b]
<u>Tableland</u>						
Median	1.16	0.07	0.71	1.72	0.5	46.72
Mean	1.41	103.1	0.84	2.66	0.56	45.69
Standard Deviation	1.24	221	0.75	2.6	0.36	19.92
<u>Sixty Lakes</u>						
Median	1.12	0.15	0.14	0.46	0.41	19.34
Mean	3.95	0.37	0.17	0.53	0.45	16.96
Standard Deviation	4.56	0.48	0.24	0.59	0.24	7.88
p-value[c]	0.29	0.71	0	0	0.31	0

a. HCH = hexachlorocyclohexane

b. DDE = dichlorodiphenyldichloroethylene

c. Mann-Whitney p-value using Chi-squared approximation

Table 13. Concentration of pesticides (ng/liter) in surface water samples collected at the Tableland (Sequoia National Park) and the Sixty Lakes Basin (Kings Canyon National Park), California, 18 - 22 August 1997 (from Fellers et al. 2004). Log K_{ow} is an indicator of the degree to which a substance will bioaccumulate. Far Pond is referred to as G-049 in the table below.

			Tableland		***Sixty Lakes***	
Compound	**Log K_{ow}**	**Limit of Detection**[a]	**G-049**	**G-054**	**S-545**	**S-471**
γ-chlordane	5.2[b]	0.03			0.27	
α-chlordane	5.2[b]	0.03				
Chlorpyrifos	4.3[b]	0.03	12	0.72	0.22	0.17
pp-DDE	6.9[c]	0.1			0.31	
o,p'-DDT	6.8[b]	0.1			0.46	
p,p'-DDT	6.9[c]	0.1				
Diazinon	3.4[b]	0.06	3.1	3.4	1.8	
α-endosulfan	3.6[d]	0.03	0.78	1	0.3	0.37
β-endosulfan	3.6[d]	0.05	0.4	0.42	1.8	0.17
endosulfan sulfate		0.03	2.9	2.2	0.33	0.4
α-HCH	3.81[d]	0.03				0.29
γ-HCH	3.8[d]	0.03				
trans-nonachlor		0.04			0.31	
Trifluralin	4.6[b]	0.1			2.5	

a. Analytical detection limit was three times the standard deviation of blank levels (LeNoir et al., 1999).

b. Selected values from Finizio et al., 1997.

c. de Bruijn et al., 1989.

d. Selected values from Suntio et al. 1988.

Figure 1. Location of the four *Rana muscosa* release sites in the Tableland area of Sequoia National Park, California. Map based on USGS 1:24000 Lodgepole, California topographic map. Contour lines are 60 feet.

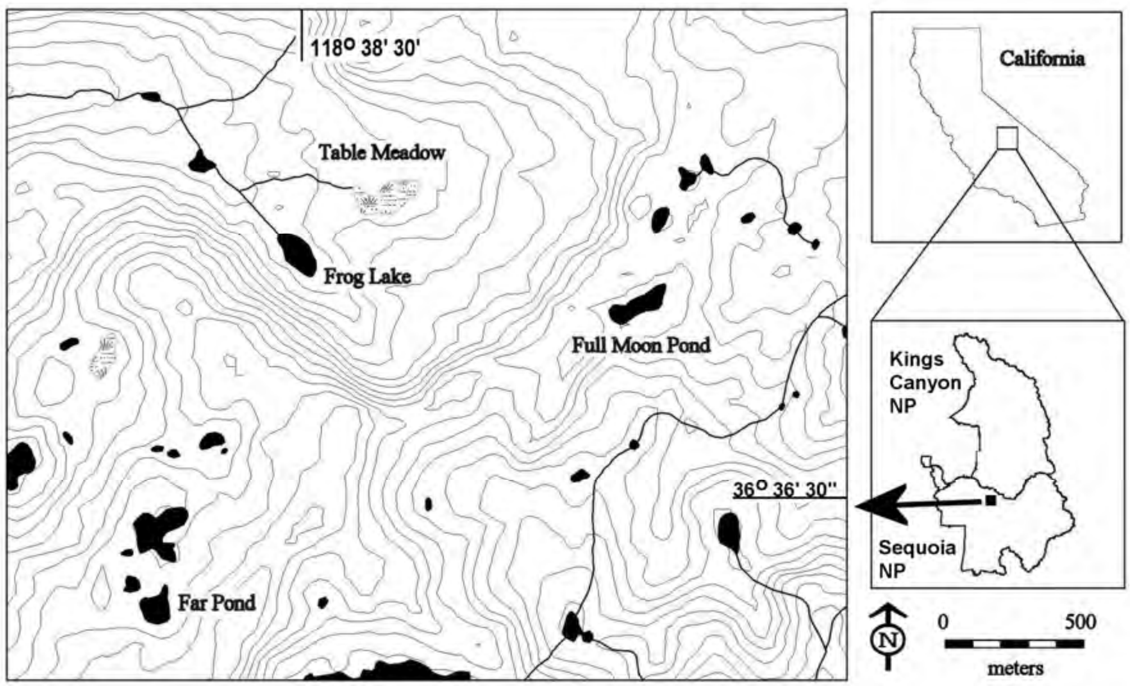

Figure 2. Counts of *Rana muscosa* at Far Pond and the adjacent dispersal ponds, Sequoia National Park, in 1994. Egg masses, second-year tadpoles, third-year tadpoles, and subadult frogs were released at Far Pond on June 14, 1994. Adult *R. muscosa* were released there on September 20, 1994. See Table 2 for numbers of each life history stage repatriated.

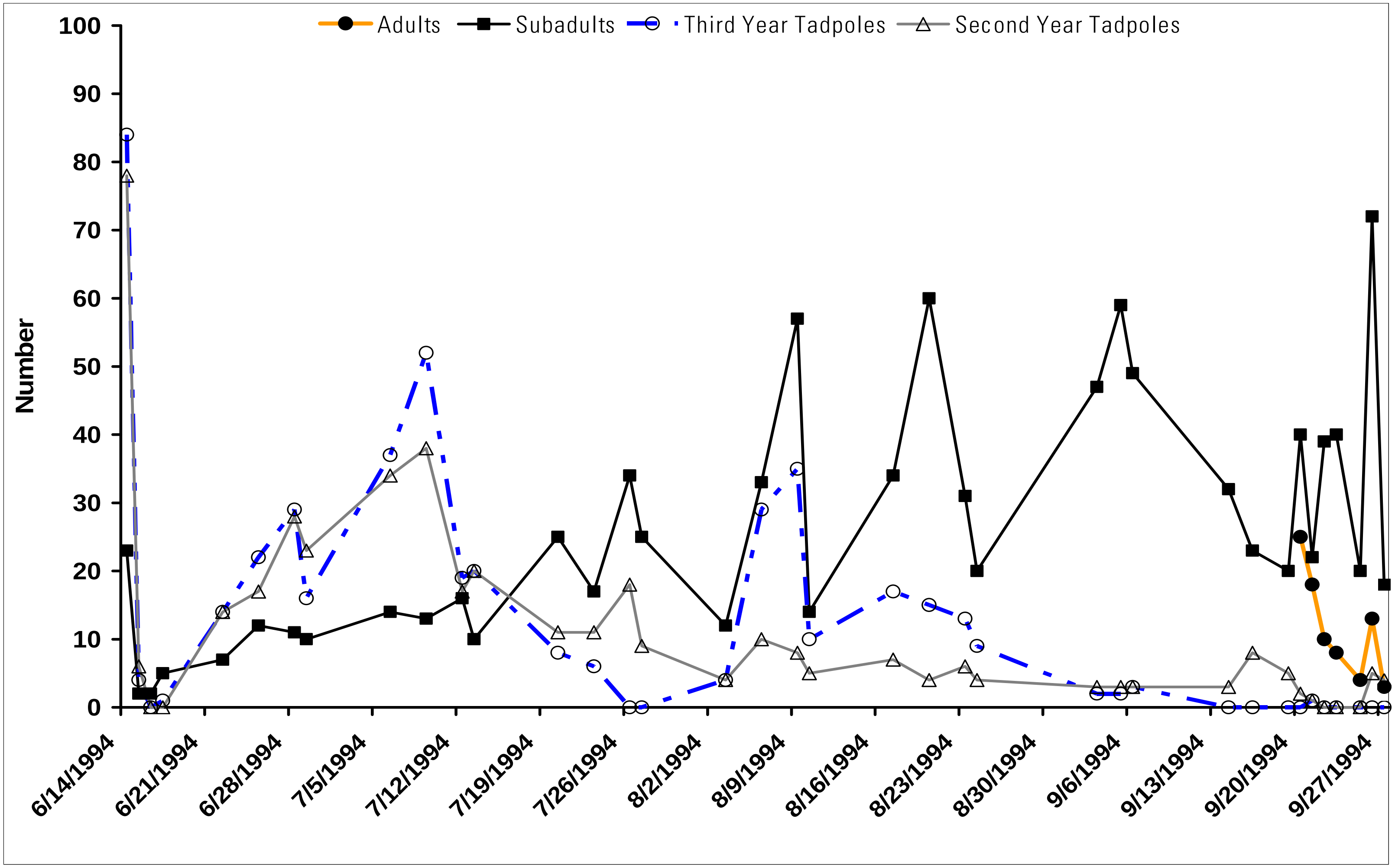

Figure 3. Counts of *Rana muscosa* at Full Moon Pond and the adjacent dispersal ponds, Sequoia National Park, in 1994. Egg masses, second-year tadpoles, third-year tadpoles, and subadult frogs were released at Far Pond on June 14, 1994. Adult *R. muscosa* were released there on September 20, 1994. See Table 2 for numbers of each life history stage repatriated.

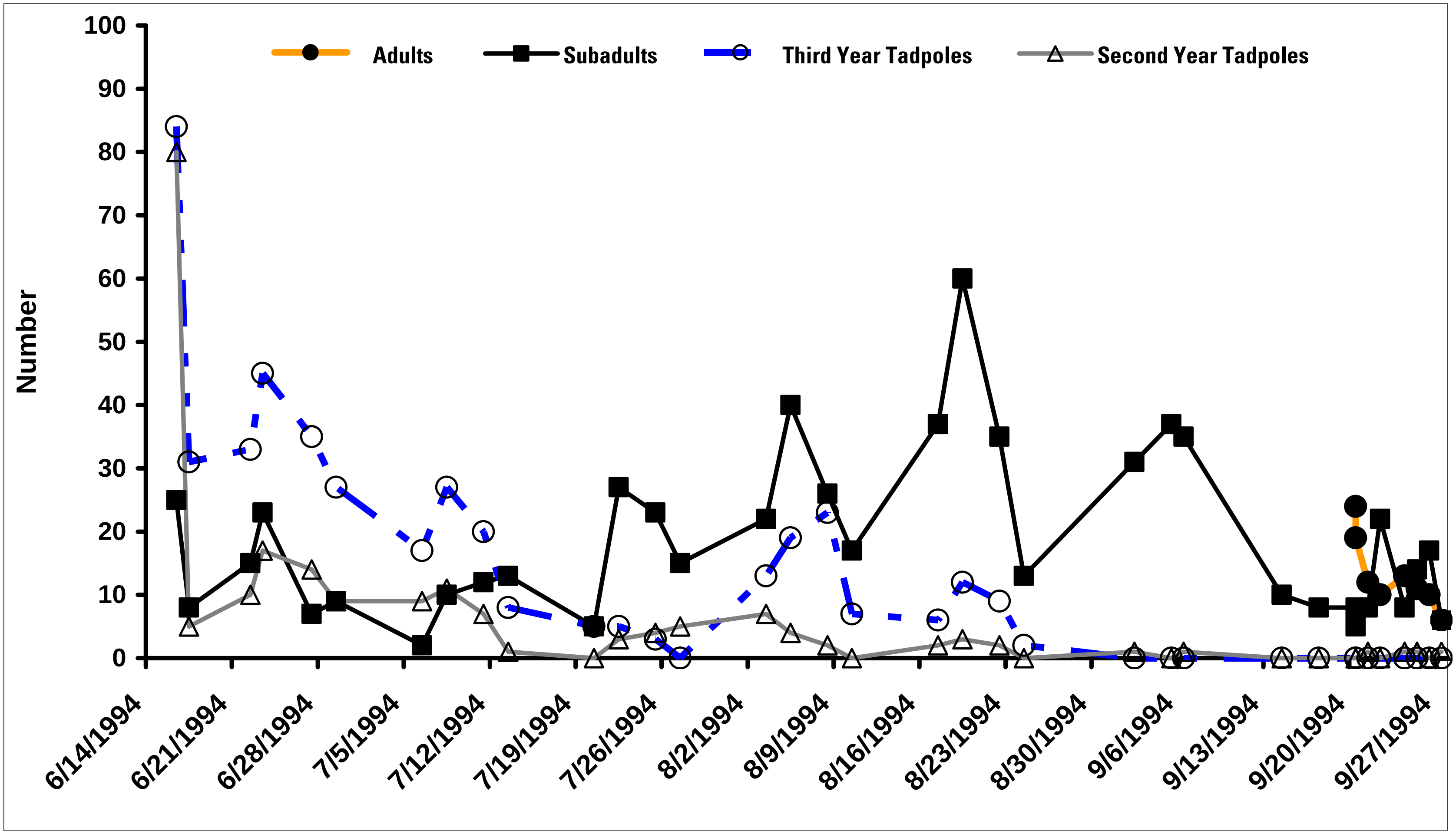

Figure 4. Counts of *Rana muscosa* at Frog Lake and the adjacent dispersal ponds, Sequoia National Park, in 1994. Egg masses, second-year tadpoles, third-year tadpoles, and subadult frogs were released at Far Pond on June 14, 1994. Adult *R. muscosa* were released there on September 20, 1994. See Table 2 for numbers of each life history stage repatriated.

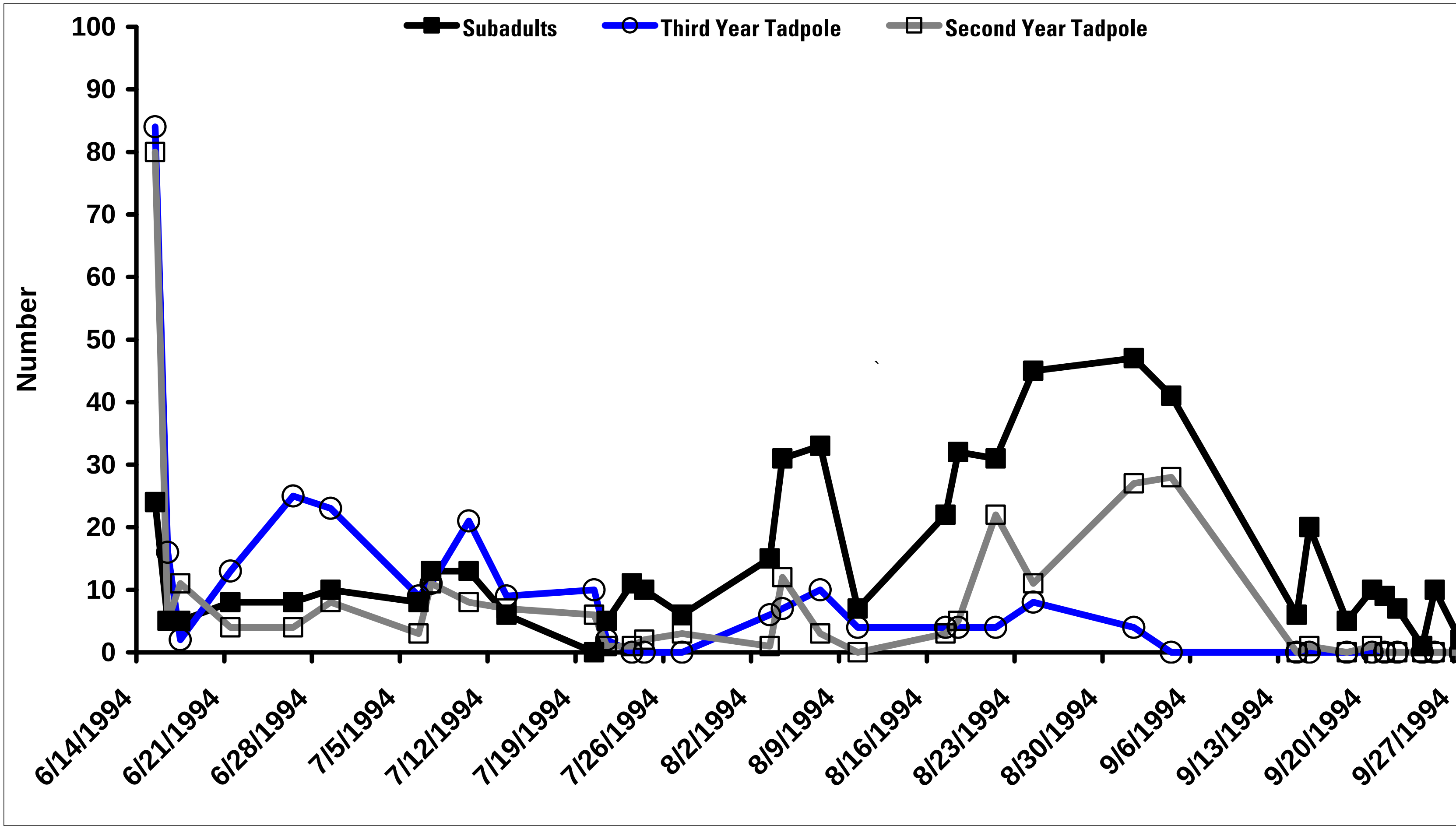

Figure 5. Counts of *Rana muscosa* at Table Meadow and the adjacent dispersal ponds, Sequoia National Park, in 1994. Egg masses, second-year tadpoles, third-year tadpoles, and subadult frogs were released at Far Pond on June 14, 1994. No adult *R. muscosa* were released there. See Tables 2 and 3 for the numbers and dates of repatriation for each life history stage in 1994 and 1995.

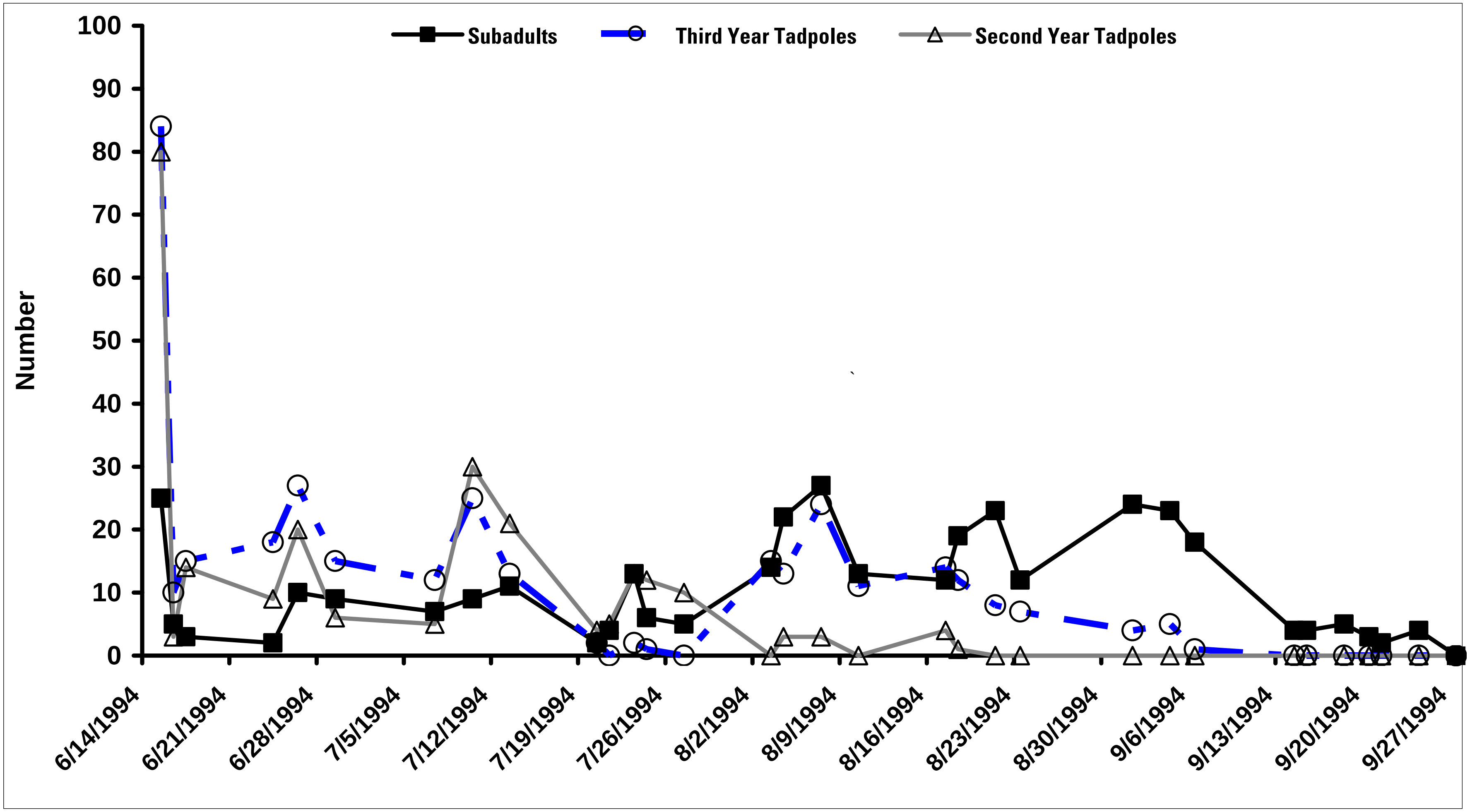

Figure 6. Counts of *Rana muscosa* at Far Pond and the adjacent dispersal ponds, Sequoia National Park, in 1995. Second-year tadpoles, third-year tadpoles, and adult frogs were released at Far Pond on August 26, 1995. See Tables 2 and 3 for the numbers and dates of repatriation for each life history stage in 1994 and 1995.

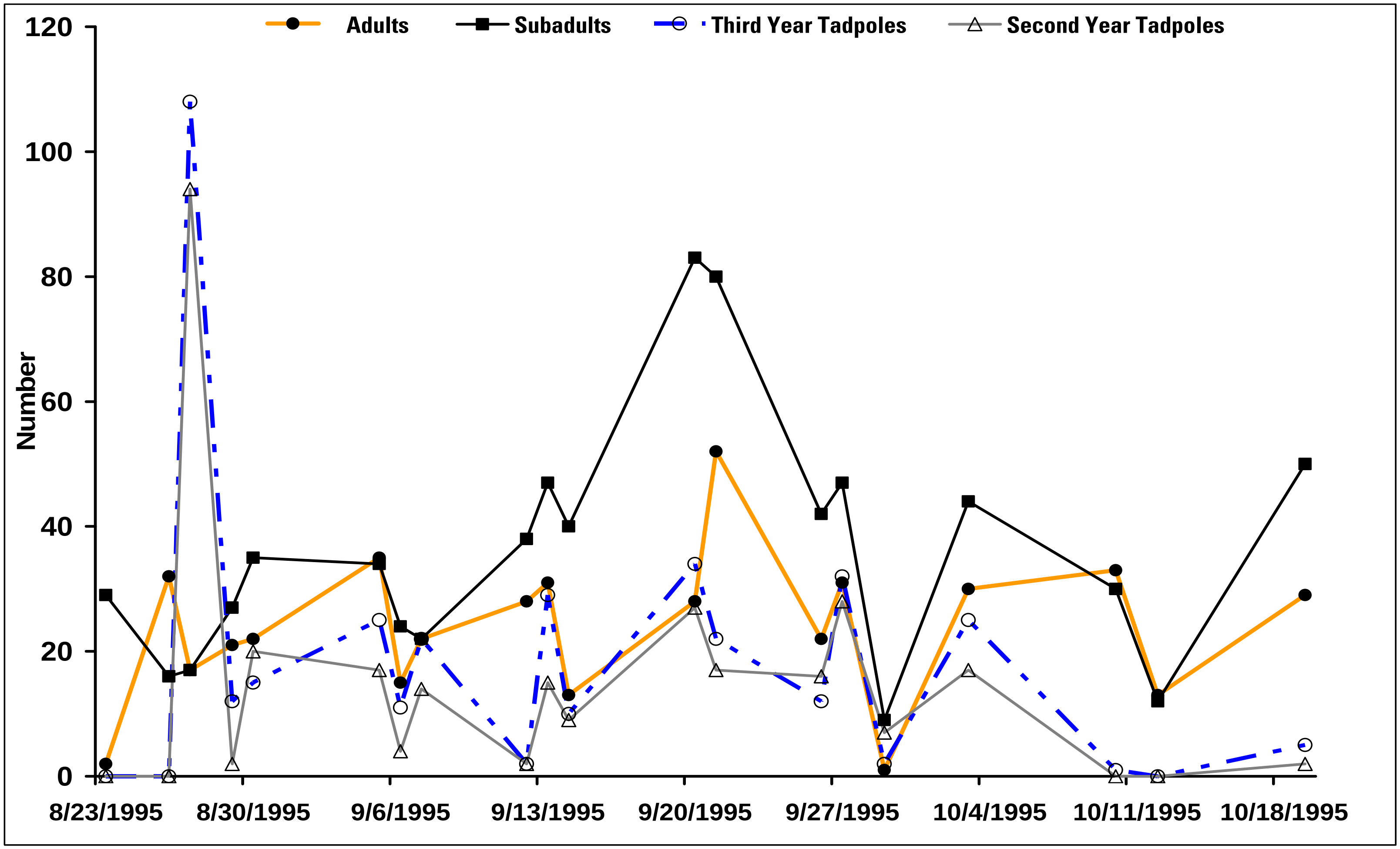

Figure 7. Counts of *Rana muscosa* at Full Moon Pond and the adjacent dispersal ponds, Sequoia National Park, in 1995. Second-year tadpoles, third-year tadpoles, and adult frogs were released at Far Pond on August 26, 1995. See Tables 2 and 3 for the numbers and dates of repatriation for each life history stage in 1994 and 1995.

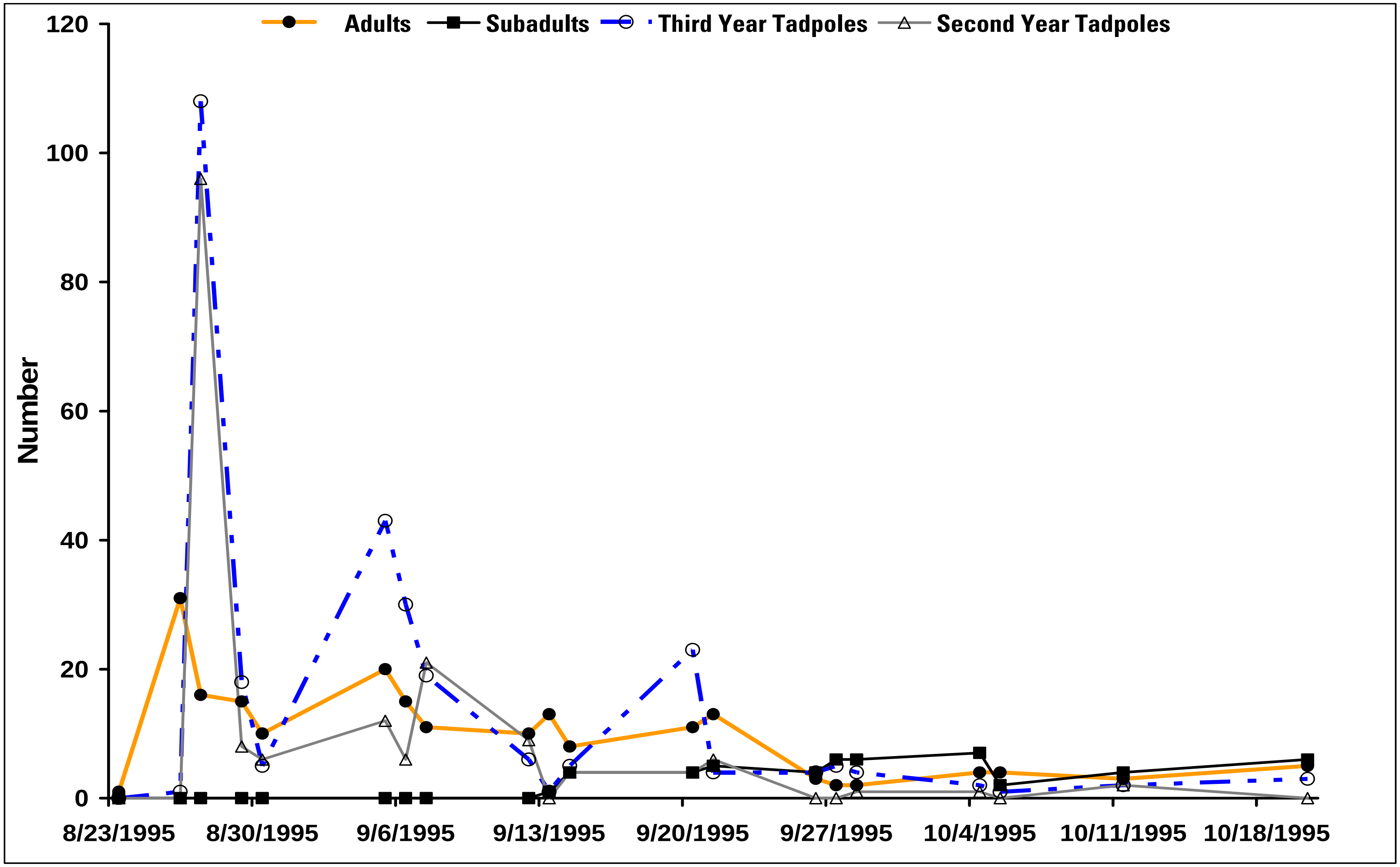

Figure 8. Counts of *Rana muscosa* at Frog Lake and the adjacent dispersal ponds, Sequoia National Park, in 1995. Second-year tadpoles, third-year tadpoles, and adult frogs were released at Far Pond on August 26, 1995. See Table 3 for numbers of each life history stage repatriated to this site.

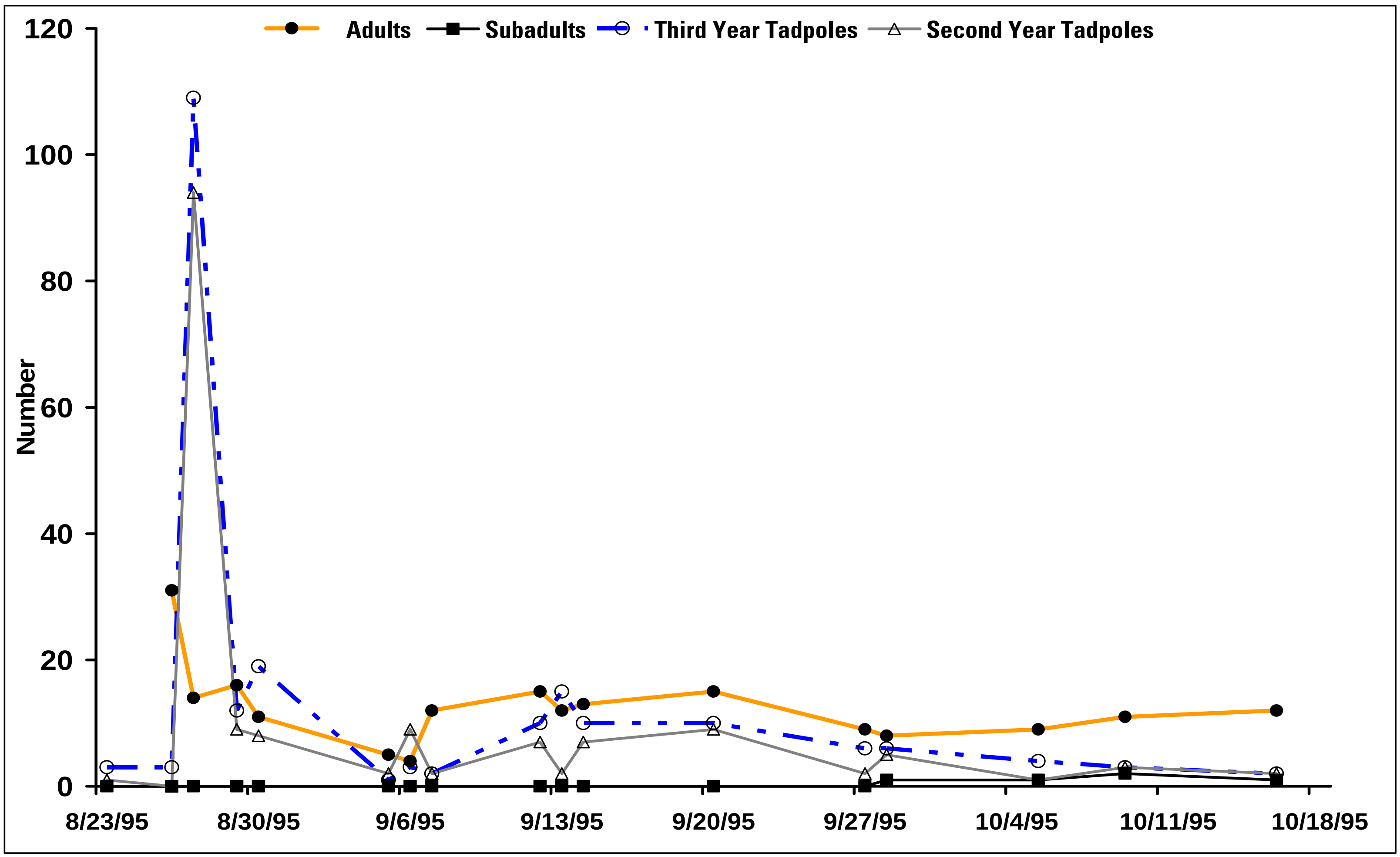

Figure 9. Dispersal of *Rana muscosa* from Far Pond, Sequoia National Park. Adjacent ponds (numbered) are referred to as Dispersal Ponds (DP). Arrows in the figures indicate the sites at which the frogs were last detected. Twelve frogs dispersed to Dispersal Pond 3, one frog to Dispersal Pond 5, and one frog to Dispersal Pond 6. See Fig. 1 for location map.

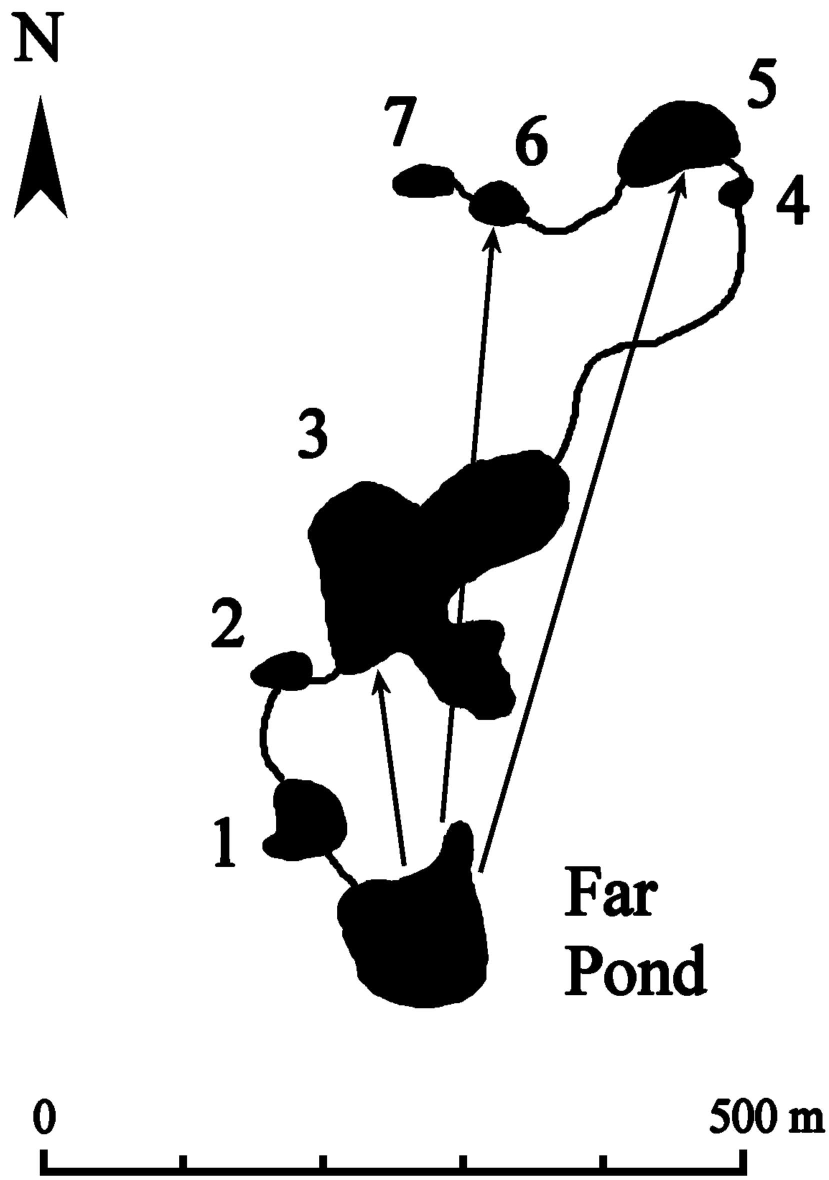

Figure 10. Dispersal of *Rana muscosa* from Full Moon Pond, Sequoia National Park. Arrows in the figures indicate the sites at which the frogs were last detected. Each arrow represents the dispersal of one frog. See Fig. 1 for location map.

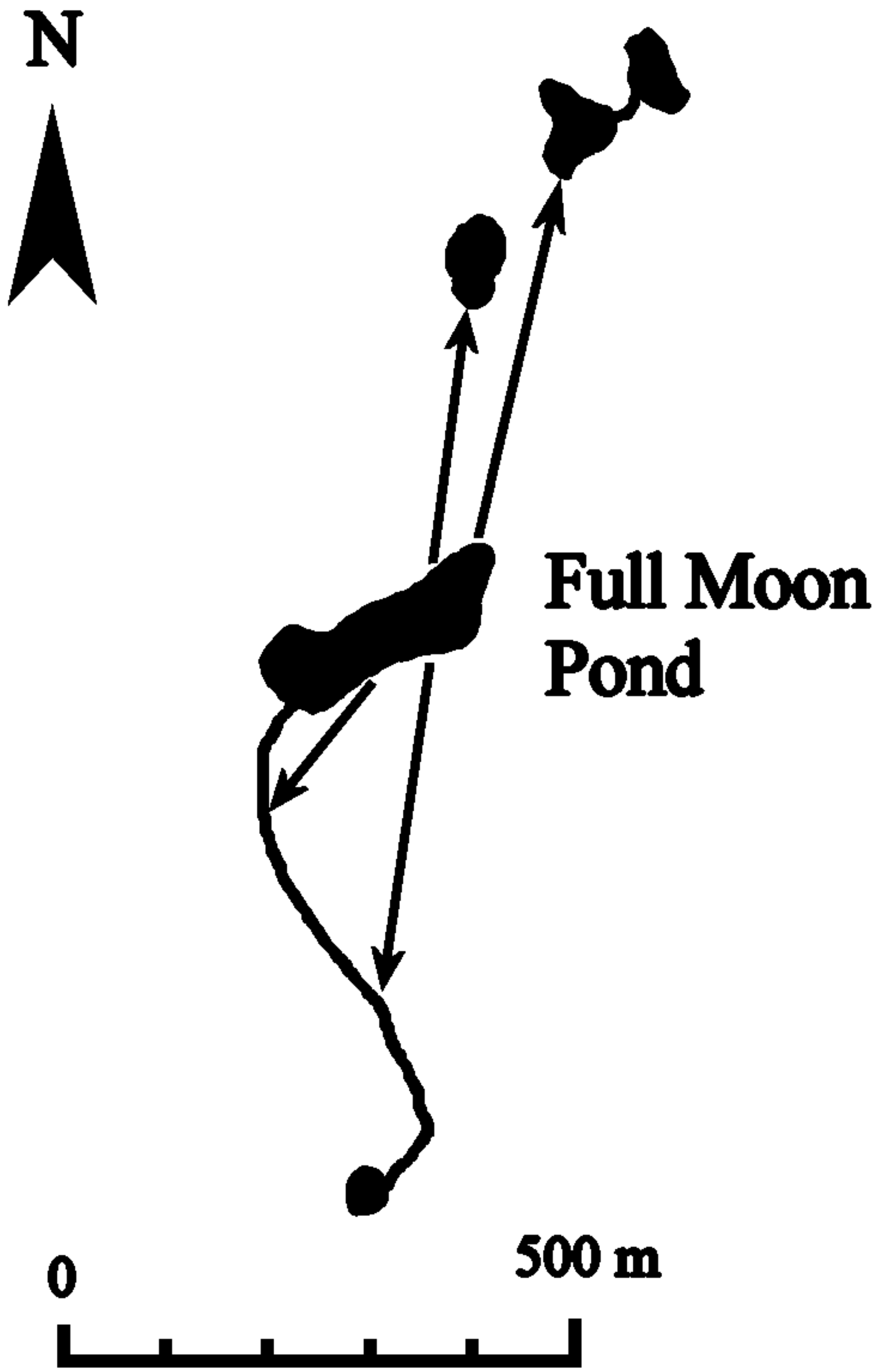

Figure 11. Dispersal of *Rana muscosa* from Frog Lake, Sequoia National Park. Arrows in the figures indicate the sites at which the frogs were last detected. Each arrow represents one frog. See Fig. 1 for location map.

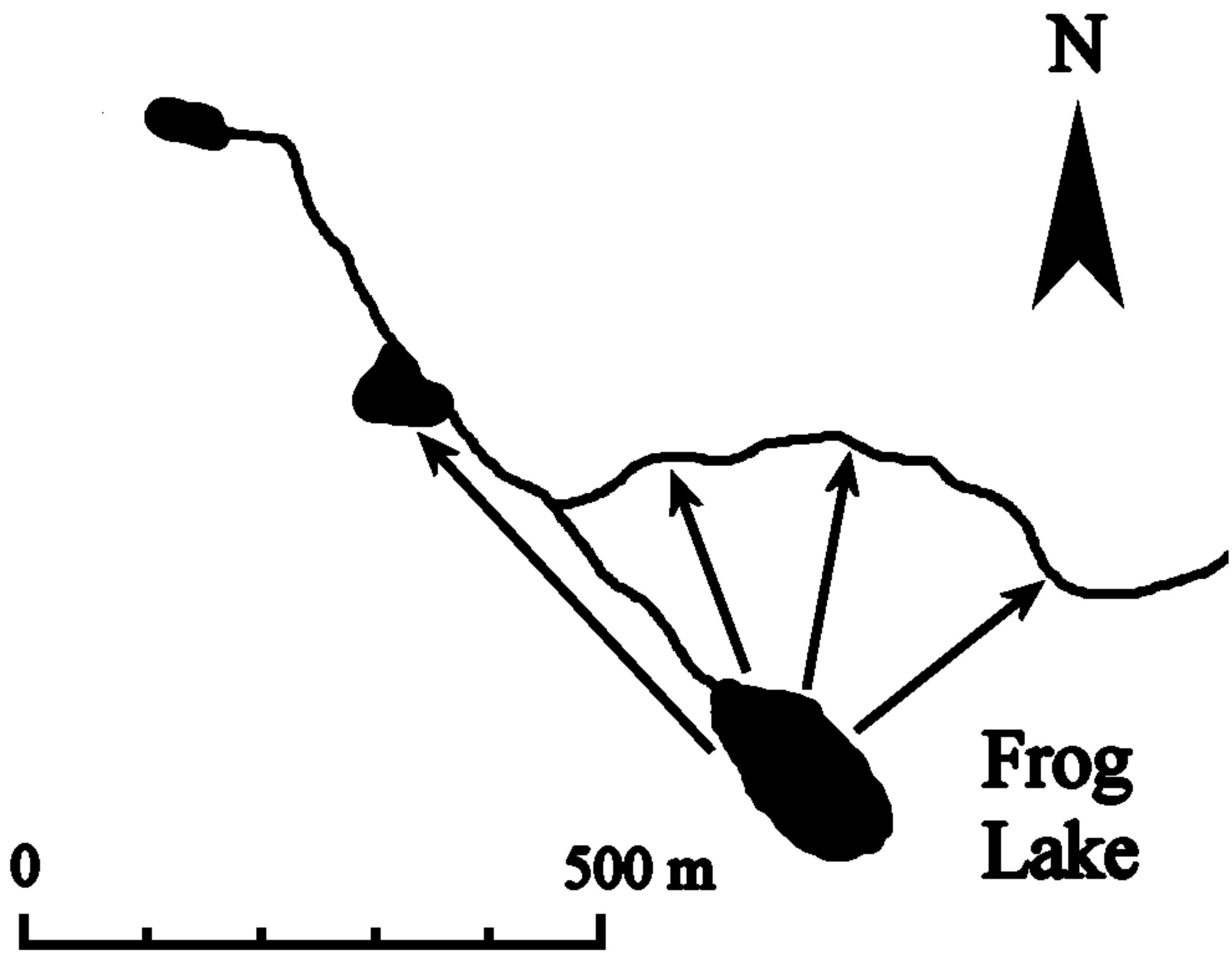

Figure 12. Frog 1760 weight (g) before and after repatriation from Sixty Lake Basin, Kings Canyon National Park, to Far Pond, Sequoia National Park. Frog was a male; SVL 4.8 cm when captured at Sixty Lake Basin on September 15, 1994. It was released at Far Pond on September 20, 1994. It had a SVL of 5.7 cm at last capture at Far Pond on August 18, 1997.

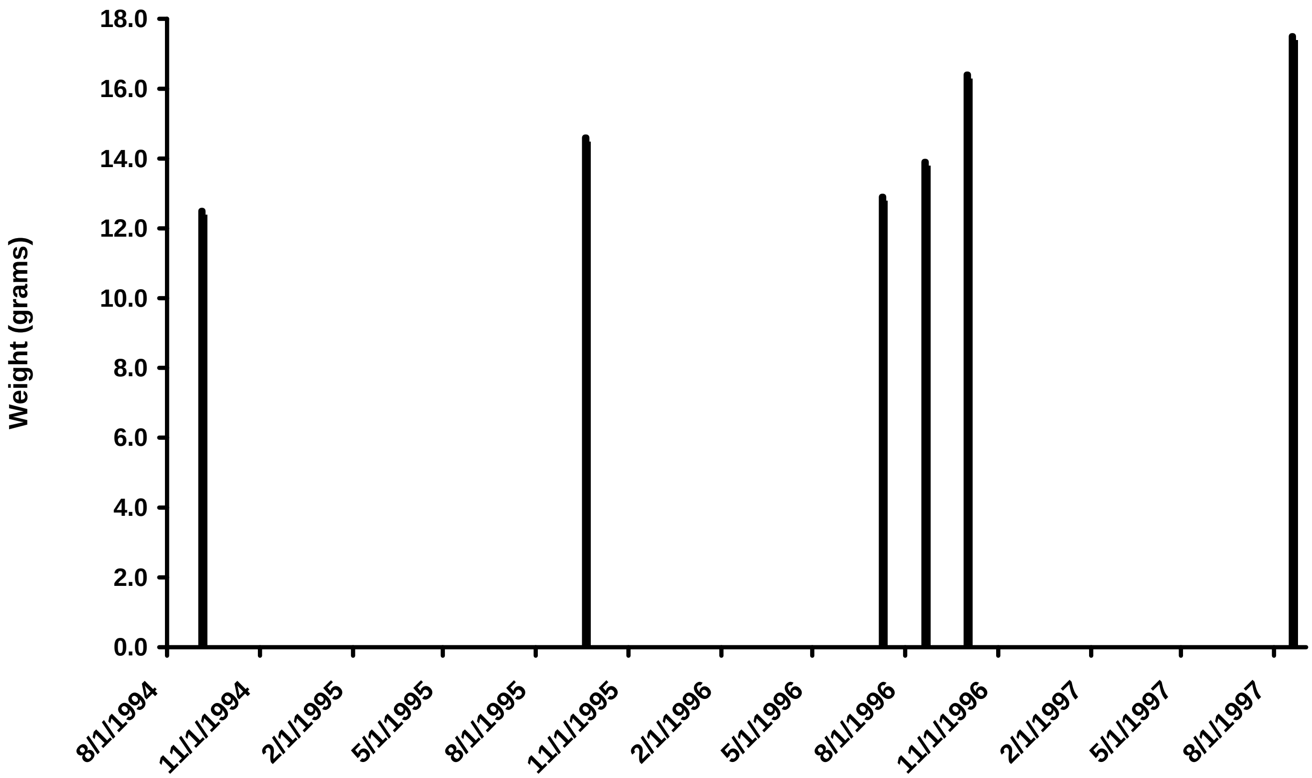

Figure 13. Frog 3173 weights (g) before and after repatriation from Sixty Lake Basin to Far Pond. Frog was a male; SVL 5.0 cm when captured at Sixty Lake Basin on August 25, 1995. It was released at Far Pond on August 26, 1995. It had a SVL of 5.7 cm at last capture at Far Pond on August 18, 1997.

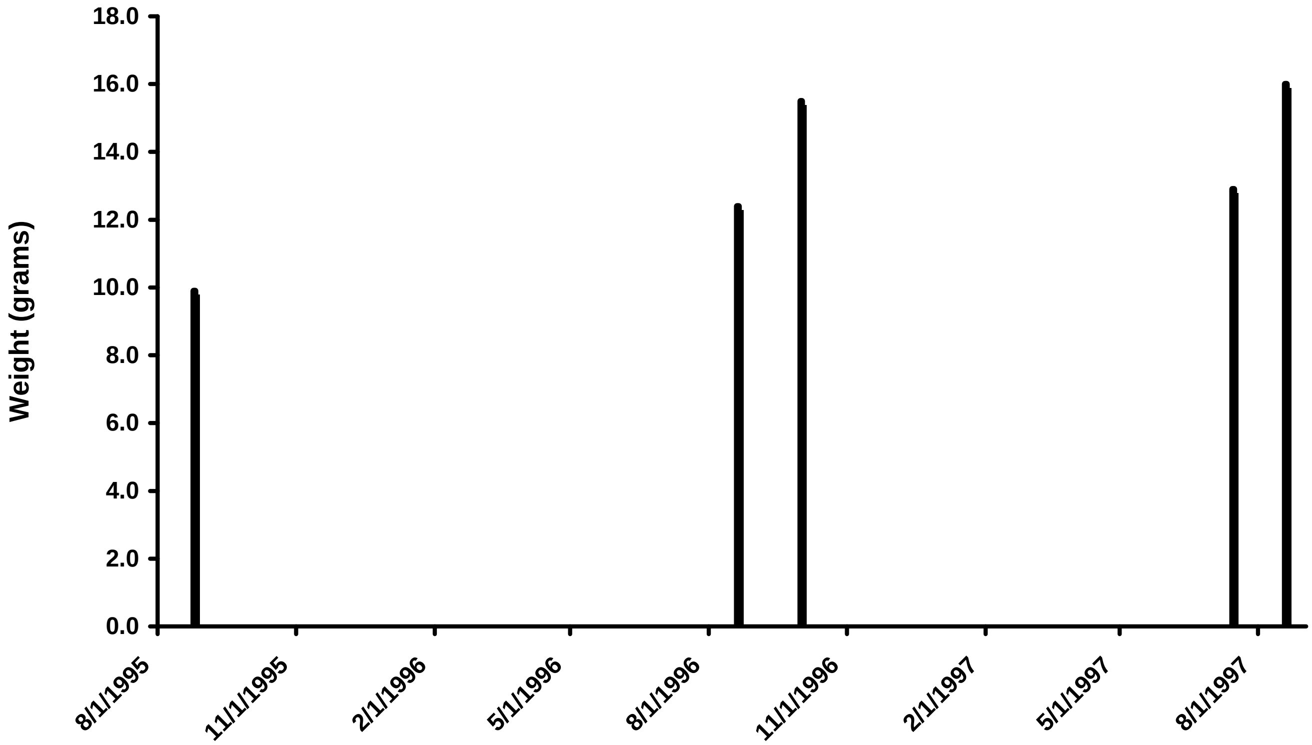

Figure 14. Water Temperatures at Far Pond, Sequoia National Park, 1994-1995. The temperature loggers were deployed at depths of 0.5 and 1.0 meters above the bottom, at a time when the water level was approximately 1.0 meter deep. The data loggers were retrieved on August 23, 1995 when the water level was approximately one meter deeper.

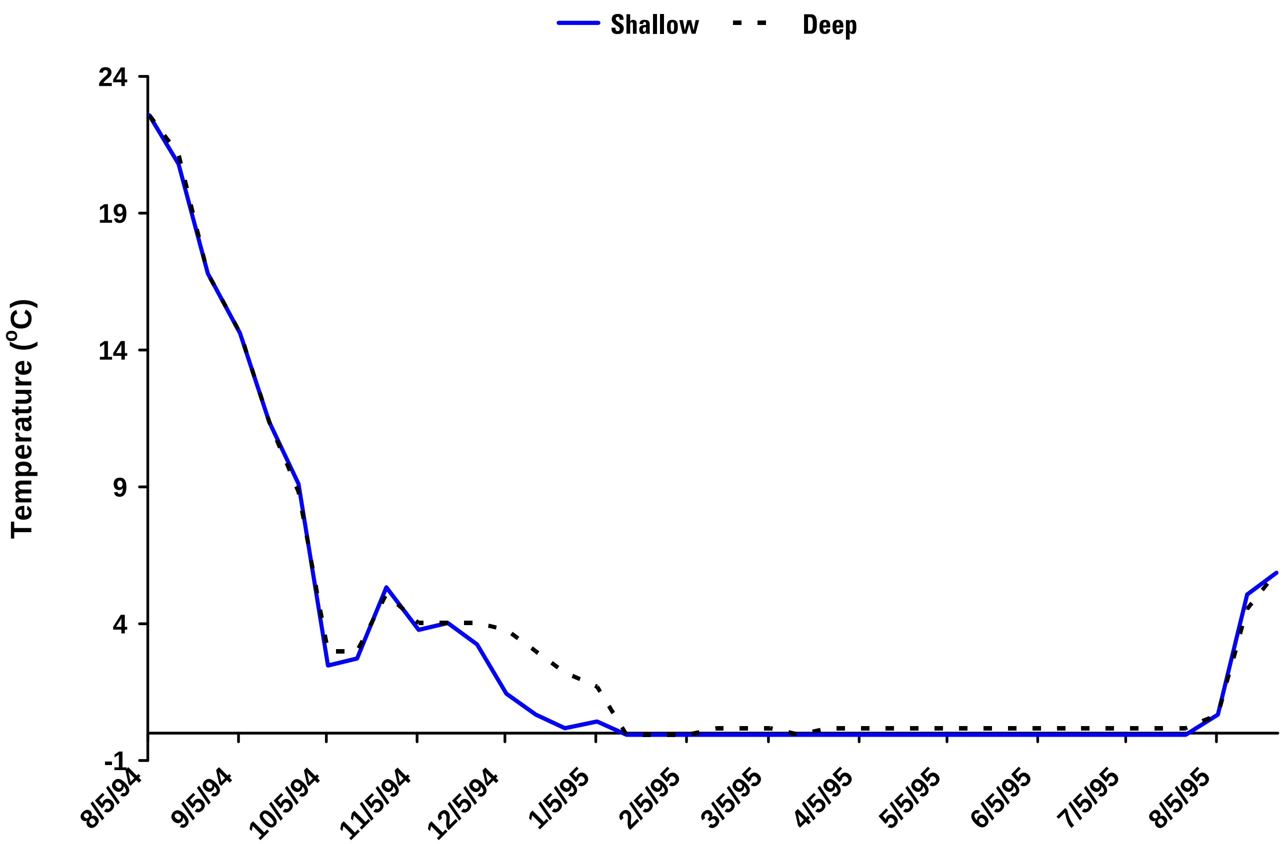

Figure 15. Far Pond, Sequoia National Park, temperature at the surface and on the bottom at the deepest point, September 26, 1995 to August 21, 1996. Darker line is temperature recorded at the surface.

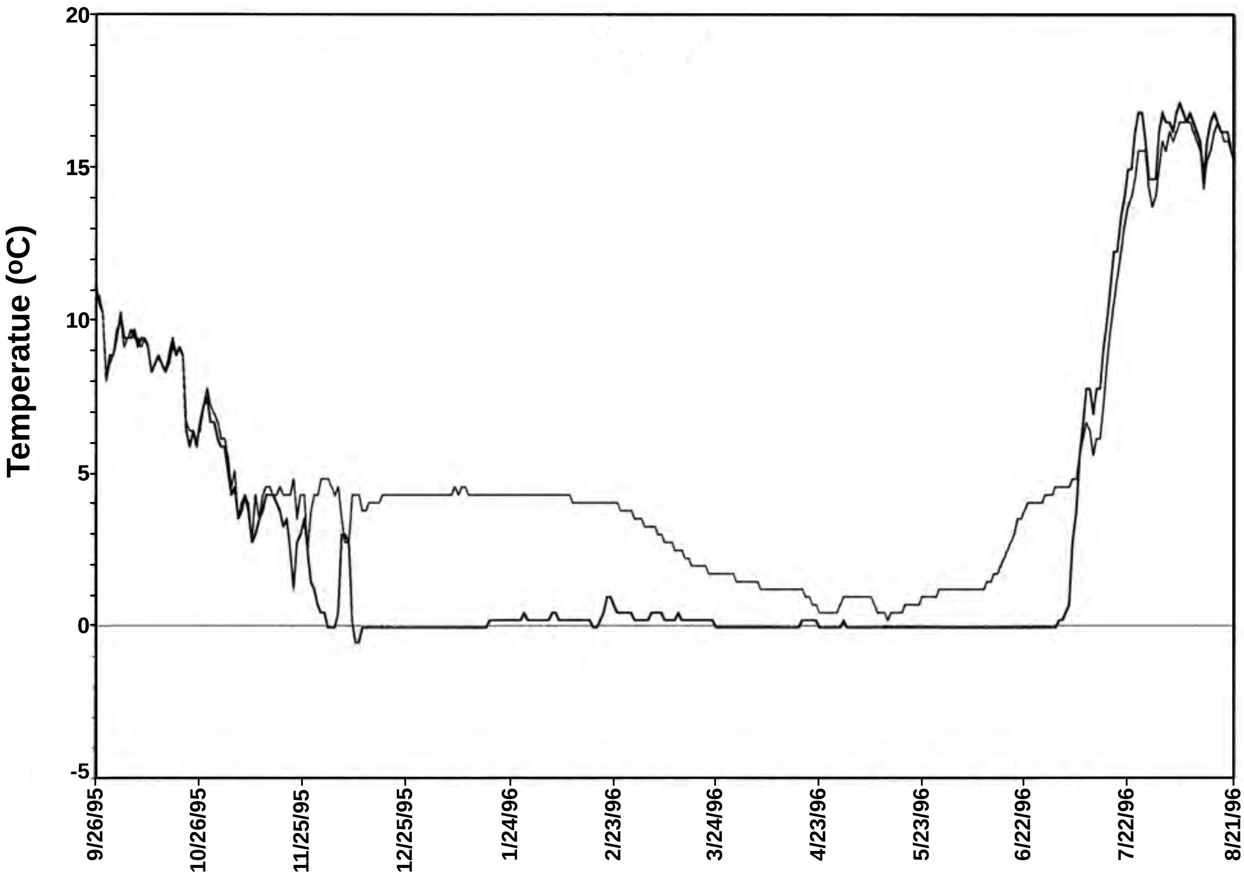

Figure 16. Full Moon Pond, Sequoia National Park, temperature at the surface and on the bottom at the deepest point, September 26, 1995 to August 21, 1996. Darker line is temperature recorded at the surface.

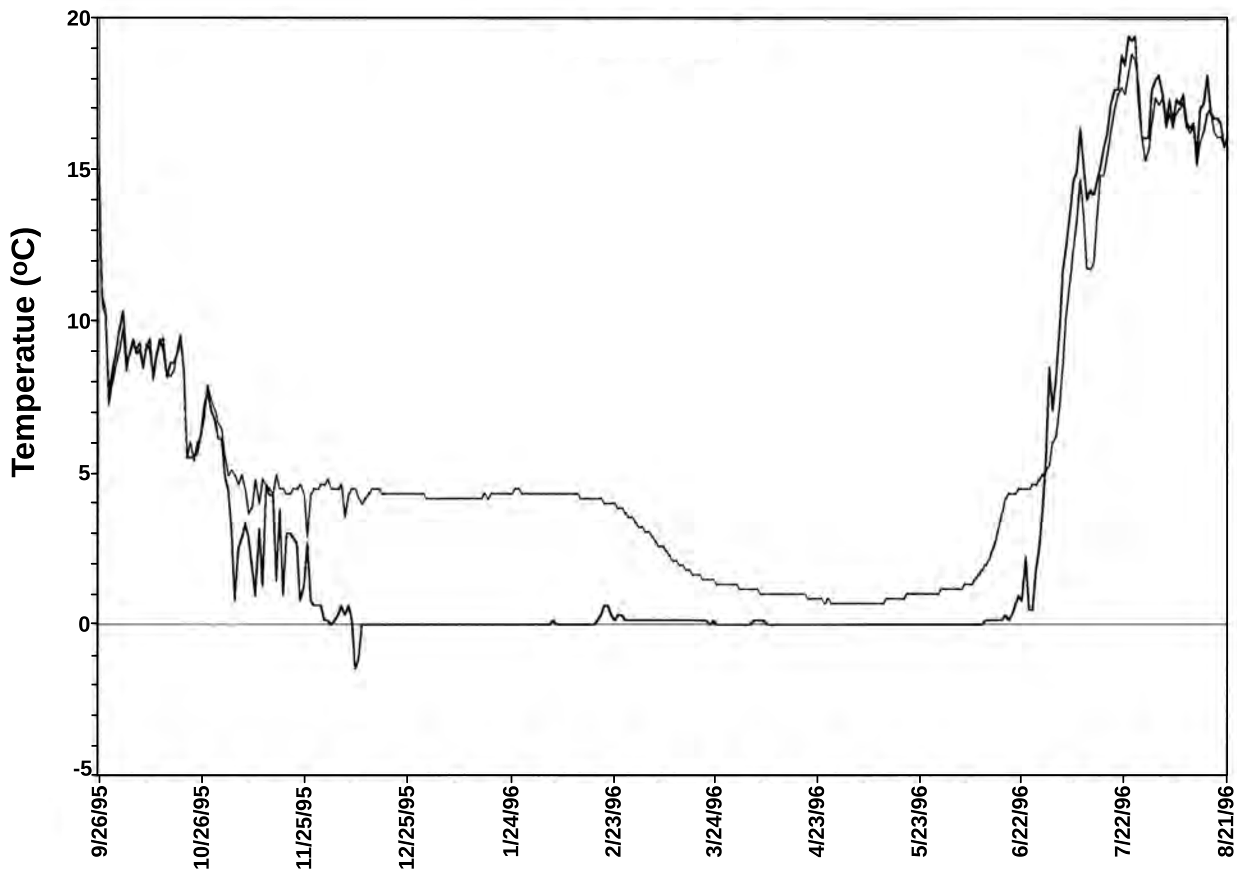

Figure 17. Frog Lake, Sequoia National Park, temperature at the surface and on the bottom at the deepest point, September 26, 1995 to August 21, 1996. Darker line is temperature recorded at the surface.

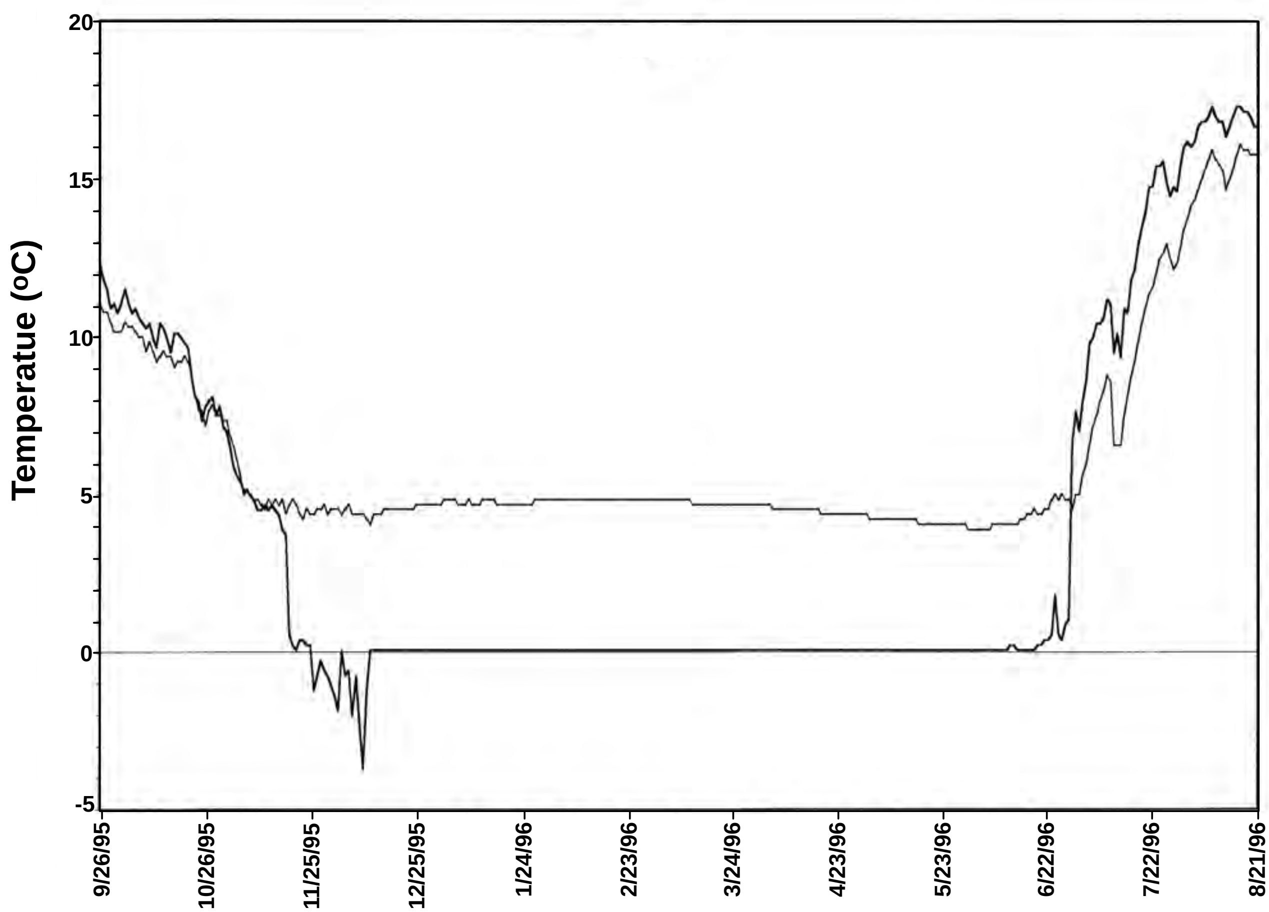

Figure 18. pH values during 1994 at the four Tableland release sites, Sequoia National Park.

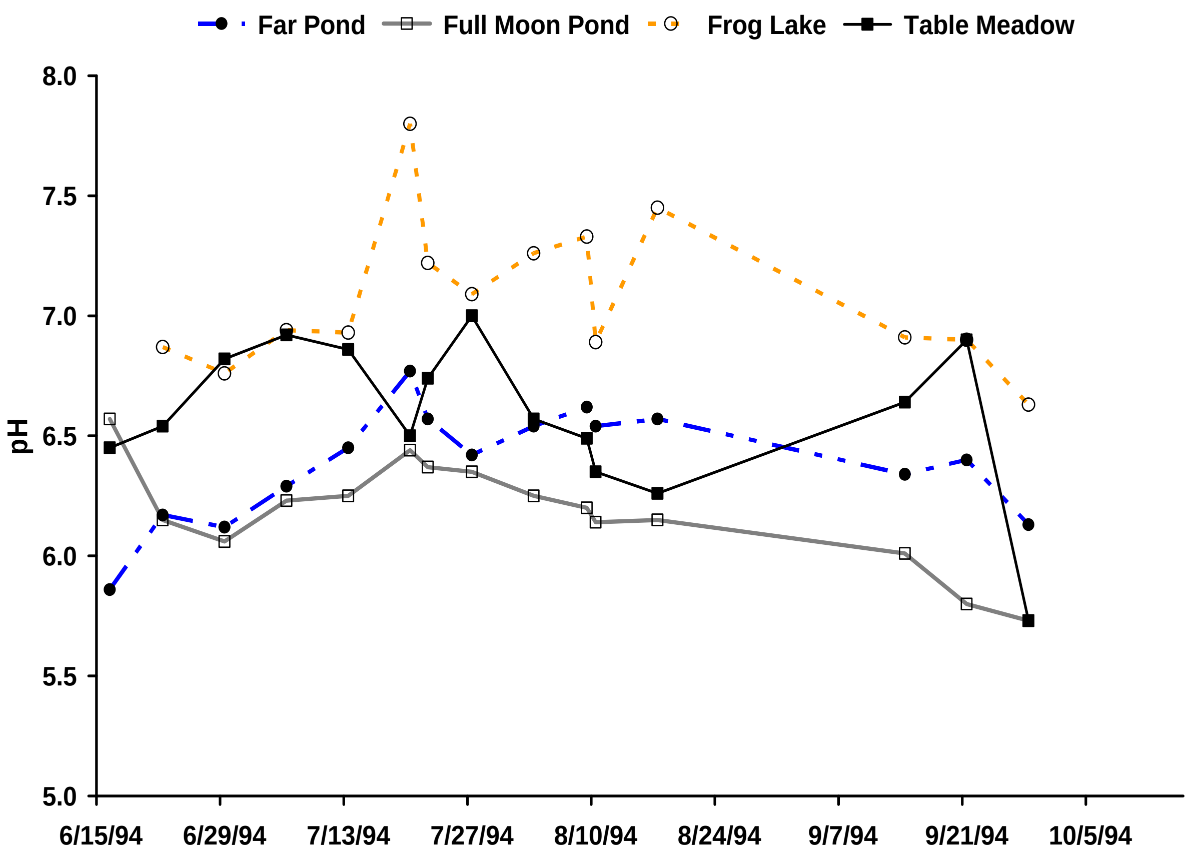

Figure 19. pH values during 1995 at the four Tableland release sites, Sequoia National Park.

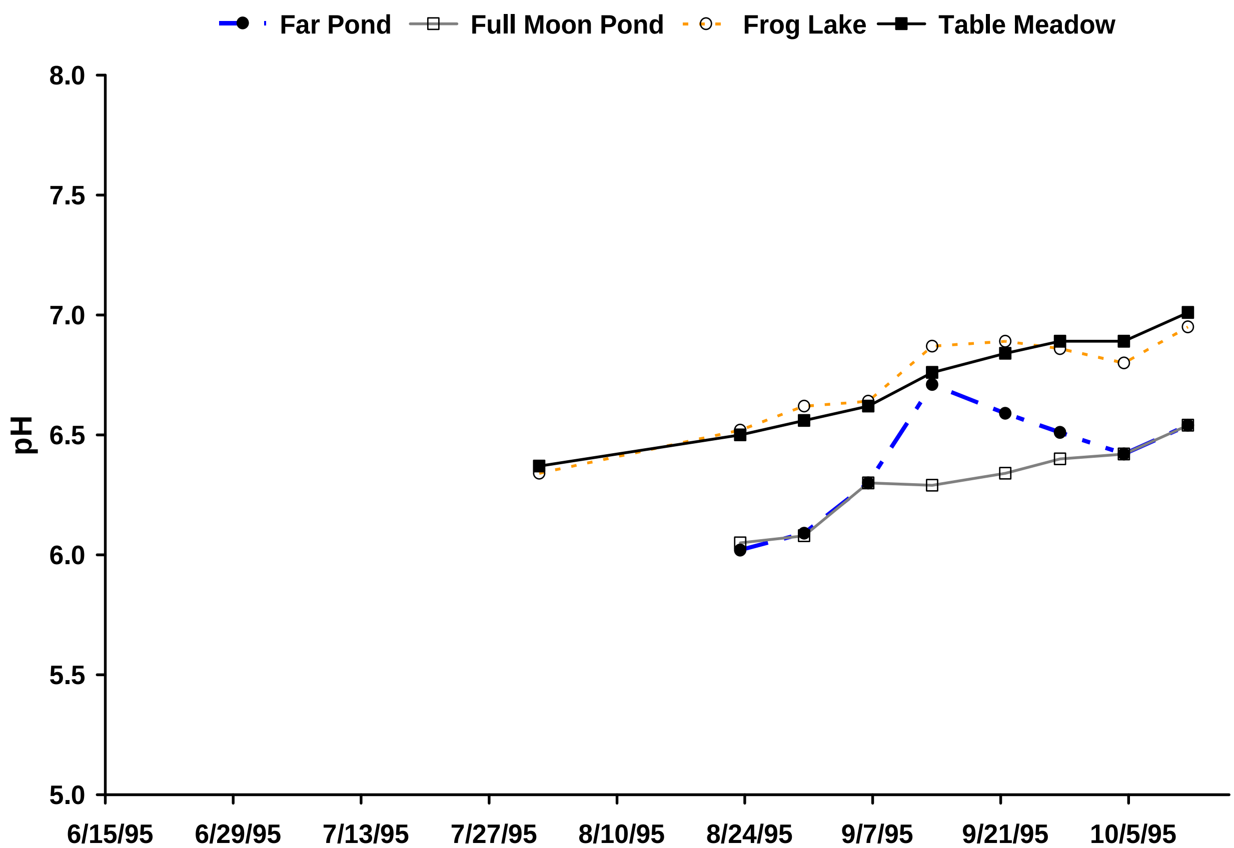

Figure 20. Electrical conductivity values during 1994 at the four Tableland release sites, Sequoia National Park.

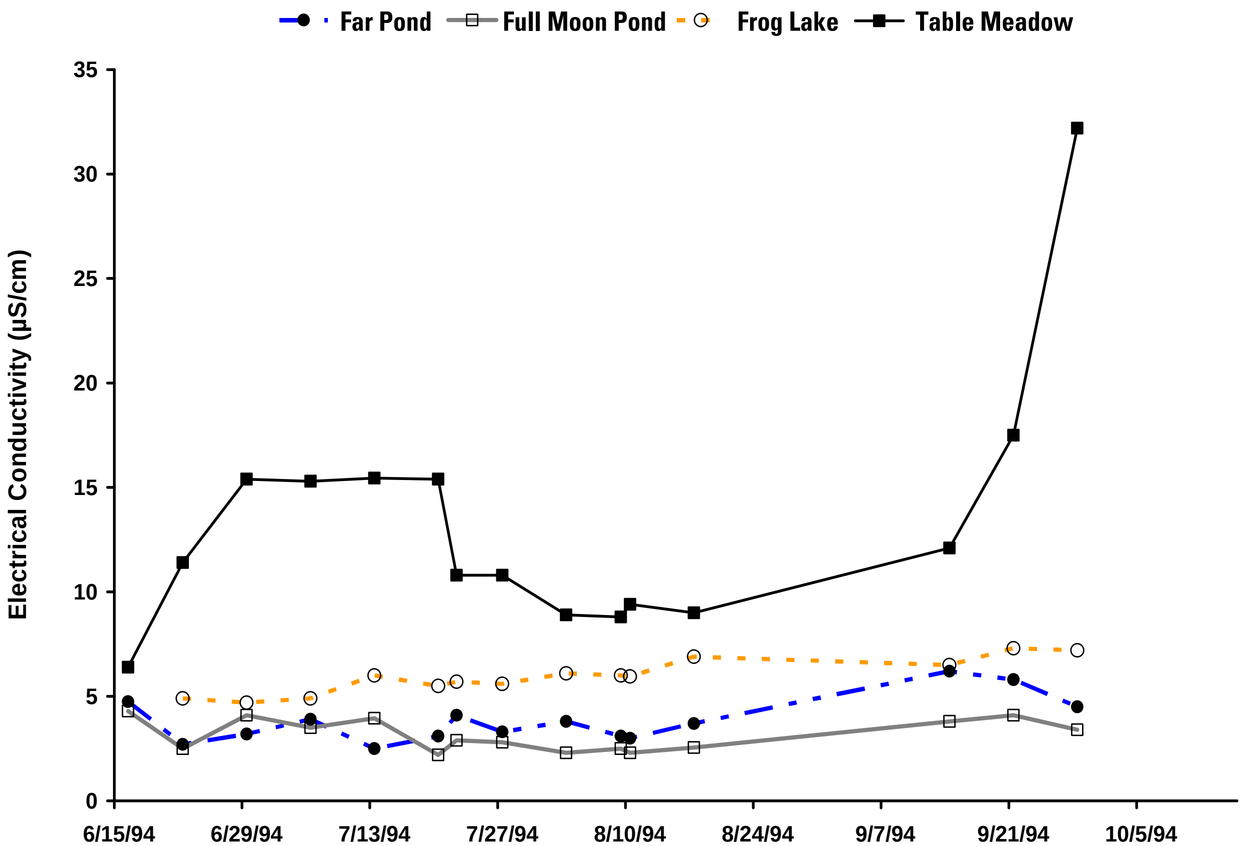

Figure 21. Electrical conductivity values during 1995 at the four Tableland release sites, Sequoia National Park.

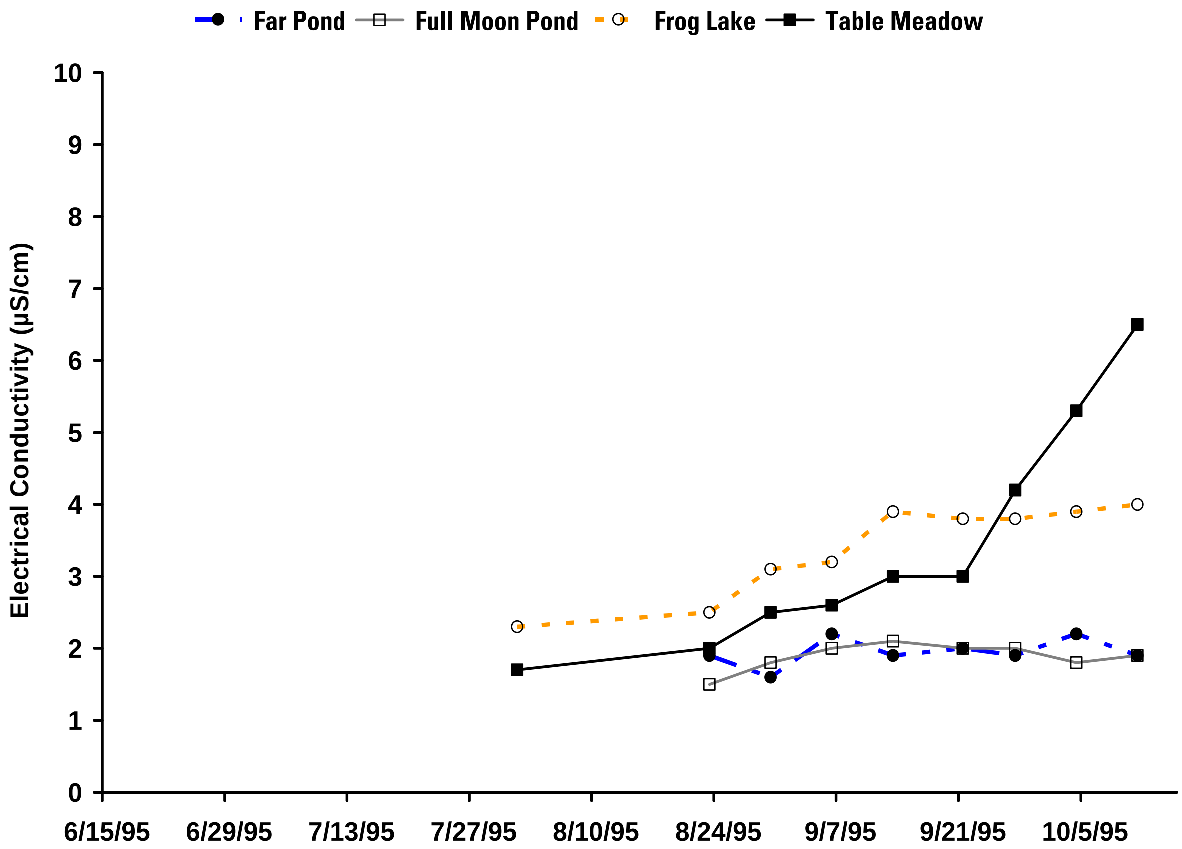

Figure 22. Departures from long-term average daily temperature and precipitation for 1993 - 1994 (measured at Grant Grove, CA, 32 km NW of the Tablelands). Temperature is ° C and precipitation is cm.

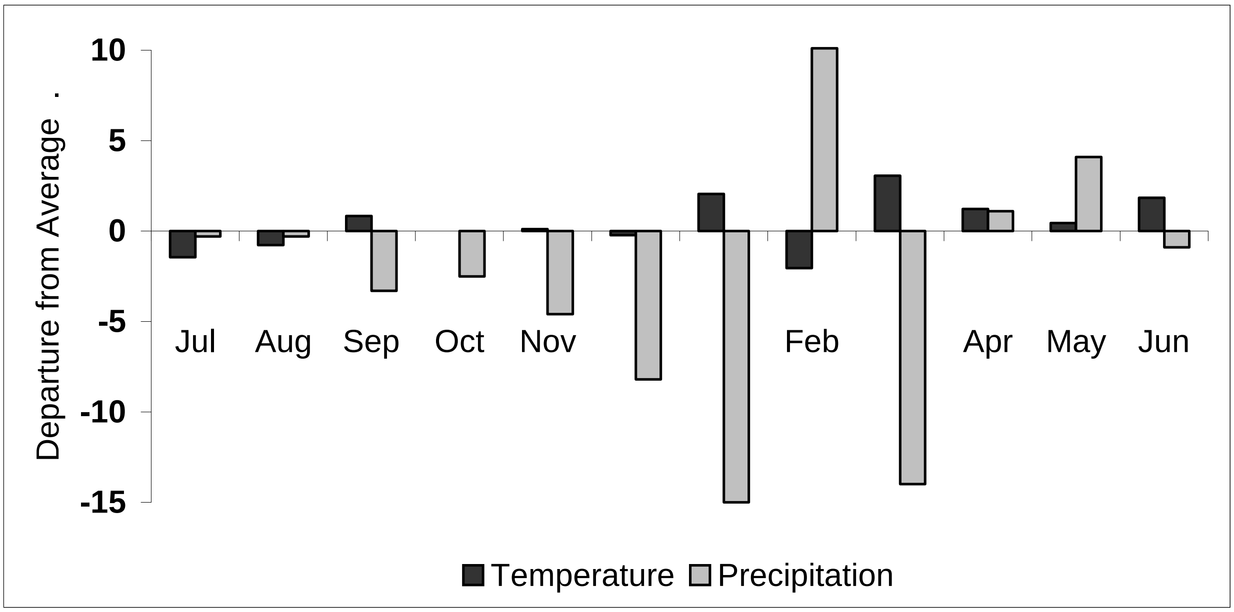

Figure 23. Departures from long-term average daily temperature and precipitation for 1994 - 1995 (measured at Grant Grove, CA, 32 km NW of the Tablelands). Temperature is ° C and precipitation is cm.