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INTERACTION OF AN INTRODUCED PREDATOR WITH FUTURE EFFECTS OF CLIMATE CHANGE IN THE RECRUITMENT DYNAMICS OF THE IMPERILED SIERRA NEVADA YELLOW-LEGGED FROG (*RANA SIERRAE*)

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Abstract.—**Between-year variation in snowpack (from 20 to 200% of average) and summer rainfall cause large fluctuations in volume of small lakes in the higher elevation (> 3000 m) Sierra Nevada, which are important habitat for the imperiled Sierra Nevada Yellow-legged Frog, *Rana sierrae*. Climate change (global warming) is predicted to increase these fluctuations, potentially leading to more frequent summer lake drying of shallow, fishless ponds where most *R. sierrae* breeding and larval development (requiring ≥ 3 years) occurs today. This study explored the interaction between water availability and the abundance and recruitment of *R. sierrae* in Dusy Basin, Kings Canyon National Park, California, USA. We mapped the Dusy Basin lakes with GPS, calculated water volumes in a low-snowpack and a high-snowpack year (2002, 2003), and counted *R. sierrae*. The lakes that dried up in 2002 were repopulated by adults in 2003, without any recruitment of metamorphosed frogs from previous year's tadpoles. The lakes that retained water, even with notable volume decreases (-60%), showed tadpole-to-subadult recruitment in the following year (2003). Similar results are obtained using data for years 1997-2006: significantly greater abundance of metamorphs in permanently wet lakes than in lakes that had dried even once during the 10 years. Similarly, those lakes that had retained water during any two preceding years had significantly more metamorphs than lakes that had dried up during that period. Our results suggest that any increase in drying of small ponds will severely reduce frog recruitment. Combined with the invasive fish that prevent frog breeding in larger lakes, lake drying may cause extinction of local frog populations.**

Key Words.—climate change; global warming; habitat; precipitation, *Rana muscosa*; *Rana sierrae*, Sierra Nevada; water

INTRODUCTION

Recent decline of numerous unrelated amphibian species (Stuart et al. 2004) has sparked research interest in both the basic ecology of amphibians, and the examination of specific factors that may be contributing to their decline (Blaustein and Kiesecker 2002; Pounds et al. 2006). In California (USA), one such amphibian is the Sierra Nevada Yellow-legged Frog (*Rana sierrae*[1], Vredenburg et al. 2007). *Rana sierrae* is endemic to the Sierra Nevada mountains and was widely distributed and common in the past, but its range has decreased by >80% in the last 90 years (USFWS 2007). *Rana sierrae*'s primary habitat consists of high-elevation lakes and slow-moving portions of streams at altitudes ranging from 1370 to 3660 m (Zweifel 1955; Vredenburg et al. 2005). Although these lakes and streams were historically fishless, hybrid trout (*Onchorynchus* spp.) have been intentionally introduced into larger lakes, where they prey on the native amphibians. The detrimental effects of fish predation on *R. sierrae* are well documented (Bradford 1989; Drost and Fellers 1996; Knapp and Matthews 2000), and it is likely that the presence of fish in a lake severely limits the use of that lake as a breeding habitat for this species. Consequently, most frog breeding in our study area is observed in smaller (fishless) lakes (Fig. 1), most of which are shallow and could occasionally dry up during the summer months. High elevation *R. sierrae* tadpoles need two to four years of permanent water to complete their larval development (Zweifel 1955; Bradford et al. 1993; Knapp and Matthews 2000). Thus, the restriction

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[1] Recent work (Vredenburg et al. 2007) has shown that species previously designated as *Rana muscosa* (Zweifel, 1955) actually comprises two species: *R. muscosa* (*sensu stricto*) and *R. sierrae*, with little or no range overlap. Thus, most extant literature (1950 – 2007) pertaining to "Mountain Yellow-legged Frog" or "*R. muscosa*" could actually refer to either (or occasionally, both) of the currently-recognized species.

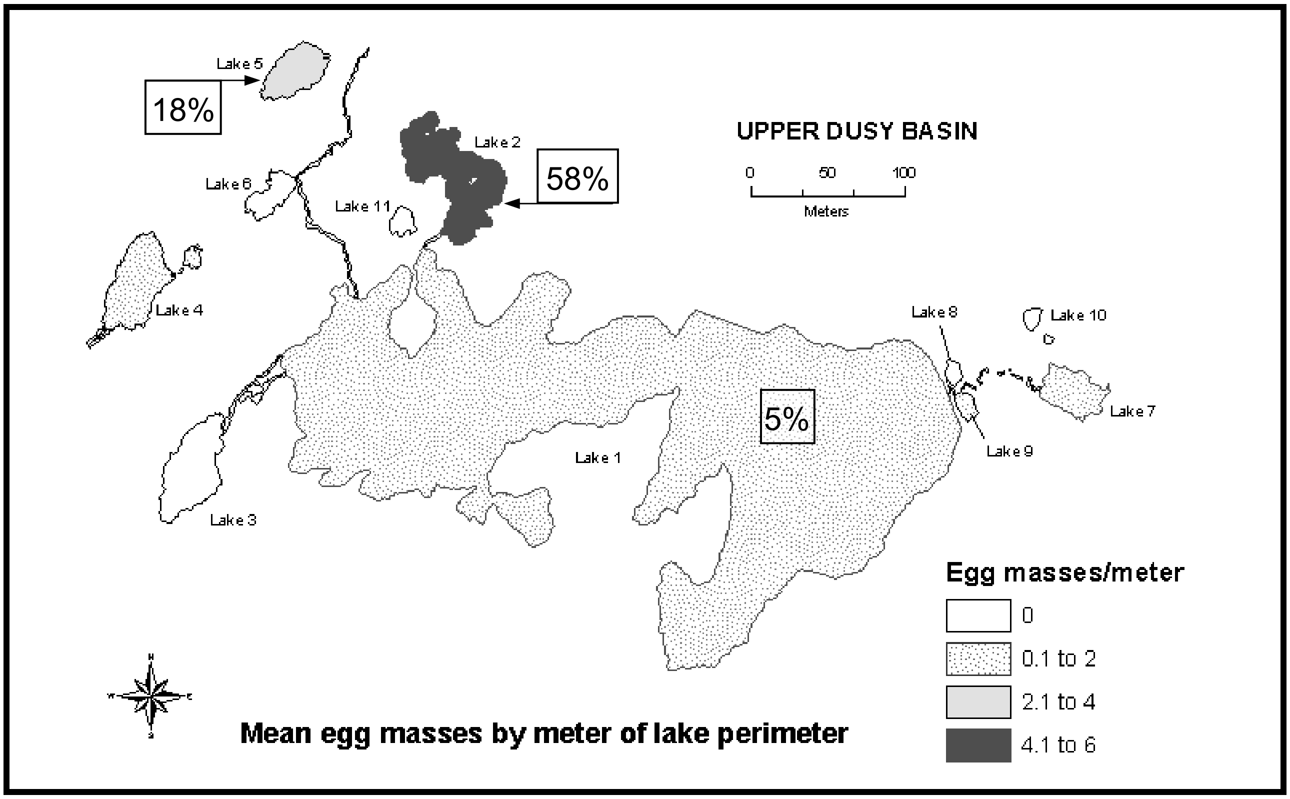

FIGURE. 1. *Rana sierrae* breeding site-preferences in upper Dusy Basin, Kings Canyon National Park, California, USA (Modified from Matthews, unpublished). Percentages in square boxes refer to the proportion of the total egg masses encountered in the basin (i.e., over half of all the egg masses in Dusy Basin were in Lake #2; only 5 % occurred in Lake #1). Note that three lakes immediately to the south (Lake #20, #21, and #22) are not shown on this map, but were also used for breeding by *R. sierrae*.

of *R. sierrae* breeding activity to semi-permanent lakes may lead to decline and extinction of local populations caused by repeated tadpole mortality during the summer lake drying. Even those lakes that do not dry completely have often lost a large proportion (> 2/3 by volume) of their water by the end of the summer. Dropping summer water levels, without complete water loss, could possibly impact the *R. sierrae* population structure and reduce survival or breeding success by greatly increasing intraspecific competition.

The persistence of water in small, high-elevation, lakes during the summer is highly dependent on the previous winter's snowpack because most of the lakes in our study area are fed by snowmelt rather than, for example, groundwater. Models have suggested that one of the principal effects of climate change on the water balance in Sierra Nevada will be a decrease in snowpack (Knowles and Cayan 2002). Half of the current snow water equivalent (SWE) is predicted to be gone by year 2090, although the loss likely will not be uniform across all elevations (Knowles and Cayan 2004). This decrease in snowpack could cause increased summer drying of small lakes, which are used for breeding by *R. sierrae*. A result could be a future increase in tadpole mortality (in small lakes), while the large permanent lakes would remain unavailable as breeding habitat because of continuing predation by the introduced trout.

The possible detrimental effects of climate change on amphibians have been outlined before (e.g., Corn 2005). However, specific climate-induced mechanisms leading to amphibian decline are still being debated (Corn 2003 vs. Blaustein et al. 2003), including the importance of water availability (Corn 2005) and potential effects of exotic species and disease (Pounds et al. 2006).

The objectives of this study were to evaluate and compare the effects of water loss during a summer and complete lake drying on frog reproduction and recruitment. We used the low-water years to examine how frog population dynamics might be affected by the combination of increased lake drying, such as might occur in the future with climate change, and the continued trout predation that prevents frog breeding in larger, permanent lakes.

MATERIALS AND METHODS

Study site.—The study was carried out in Dusy Basin, where *R. sierrae* population monitoring has been

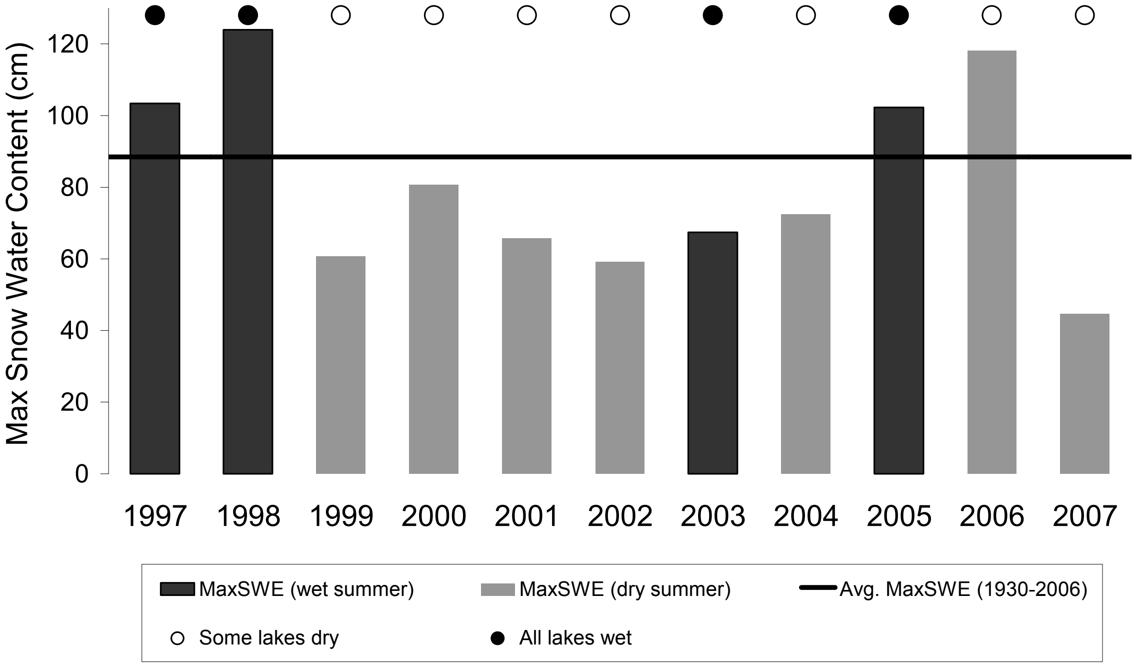

FIGURE 2. Snowfall data from the automated sensor at Bishop Pass, together with a "summer-rainfall indicator" and a lake drying symbol. Bar height denotes the maximum snow recorded that year (in cm of "snow water equivalent", SWE; the actual depth of snow is about three times the SWE); the 1930-2006 average max. SWE (88.47 cm) is shown as a horizontal line. Bar color indicates summer rainfall (dark – normal, gray – low summer rainfall); circles represent summer lake drying (filled circle: all lakes retain water; empty circle: ≥1 lake dried during summer) Notice the large range in amount of snow from year to year, and a matching trend in the low summer rainfall (light gray bars) and drying of at least one breeding lake (open circles).

ongoing since 1997. Dusy Basin, located in the northeastern corner of the Sequoia and Kings Canyon National Parks (SEKI), California (37º5'40" N, 118º33'45" W; elevation 3470 m), is typical of the high-altitude glacial basins in the Sierra Nevada in having only incipient soil development and minimal plant cover of herbs, sparse shrubs, and Whitebark Pine (*Pinus albicaulis*), which are limited by the granitic substrate and short growing season. The basin consists of a cluster of 15 lakes and six small streams (Fig. 1). Most lakes are small, shallow (< 1 ha, < 2 m depth), clear, and oligotrophic. Some lakes may dry up during the summer, and all freeze over during the winter, with some freezing through to the bottom. Lake fauna includes aquatic macroinvertebrates (i.e., amphipods, isopods, insects, annelids), two species of frogs (*R. sierrae* and Pacific Treefrog; *Hyla regilla*), and one species of aquatic snake that preys on the frogs, the Mountain Garter Snake (*Thamnophis elegans elegans*). All Dusy Basin lakes were historically fishless, but the largest, deepest lake (Lake #1), and water bodies downstream of it (Lake #3), today support a breeding population of introduced trout (*Onchorynchus* spp.).

Climate data.—To evaluate the yearly snowfall during the study, we used the data from an automated snow-weight sensor (the "Bishop Pass" sensor; #222, code "BSH") located at the southwestern edge of the Dusy Basin (37°6'0"N, 118°33'25.2"W). The snow water content data from this sensor (Fig. 2) were obtained directly from the Cooperative Snow Survey website (http://cdec.water.ca.gov/cgi-progs/staMeta?station_id= BSH). We also used this yearly snow-sensor data to evaluate the relationship between increased snowfall levels and *R. sierrae* breeding effort. We compared the yearly highest recorded number of tadpoles ("MaxTadpoles") with the preceding winter's snowpack, and described the snow-tadpole relationship using a cubic smoothing spline function within a generalized additive model (Hastie et al. 2001).

To compare the summer rainfall during the study with the average rainfall in the area, we calculated a long-term (1930-2006) average of summer rainfall (the sum of mean rainfall values for the months July, August, and September) from the nearest rainfall sensor (Lake Sabrina sensor; website as above, sensor code "SBN"). In addition, we deployed a recording rain gauge (HOBO

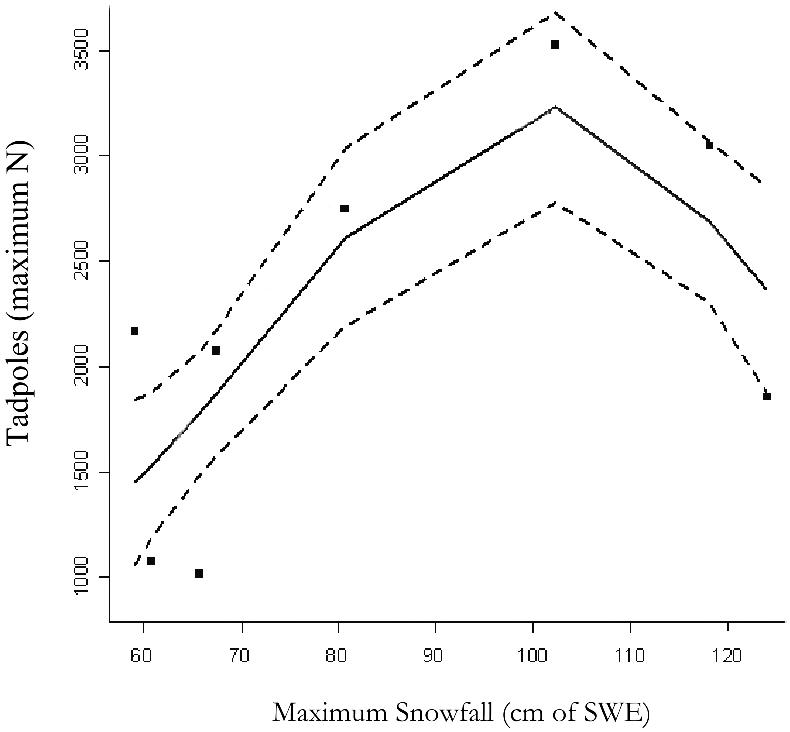

FIGURE 3. *Rana sierrae* breeding effort ("MaxTadpoles" - the maximum recorded number of tadpoles in a year) plotted as a function of the yearly snowpack (in cm of SWE). Solid line: nonparametric fit ($r^2 = 0.1$); dashed lines: 95% CI. The highest breeding effort was observed around 100 cm SWE, which is well above the long-term average snowpack of 88.5 SWE.

Recording Rain Gauge) in Dusy Basin to measure rainfall during the field data collection in the summer.

The Dusy rain gauge data (not shown, used solely to determine "dry summers," see below) were then compared with the long-term average (1930-2006) from the Lake Sabrina sensor, to determine whether the years during the study included a "dry summer" (defined herein as a summer when the Dusy rainfall totaled < 90 % of the long-term average). We hypothesized that during the "dry summers" more lakes would be expected to dry up than during a normal summer, when the lake persistence would be primarily a function of the preceding winter's snowpack.

GPS lake mapping.—To determine how lake drying affects the *R. sierrae* population over multiple years, we noted whether or not water was present in each lake (wet/dry) at the end of the summer (for years 1997-2006). Additionally, to evaluate how the variation in water level, without complete lake drying, affects the *R. sierrae* population, we quantified lake-level changes during the summer by mapping the lakes using a global positioning system (GPS) and calculating the water volume.

To measure the changes in water volume, as well as the changes in water surface area and shoreline length, we used a GPS receiver to map the bathymetry (underwater topography) and perimeter of each lake as water receded during the summer months. We re-mapped the lake perimeters multiple times during each field season, immediately following a *R. sierrae* count in each lake, so that frog survey data could be related to physical habitat data (water volume). We used a Trimble ProXRS GPS receiver (Trimble Corporation, Sunnyvale, CA) with real-time differential correction (Omnistar Inc, Houston, TX), accurate to about 30 cm horizontally. We used the measured lake depth to generate bathymetry, and employed a "surface area matching" method to track volume change between years (see details in Lacan et al. 2006). We plotted the lake maps with ArcGIS 9.1 software (ESRI Corporation, Redlands, California, USA).

Quantitative description of lake drying.—We devised two metrics to describe a lake's "drying behavior." The first metric was a lake's *permanence rank* (PR; from 1 to 5), which we obtained by ranking the lakes based on the

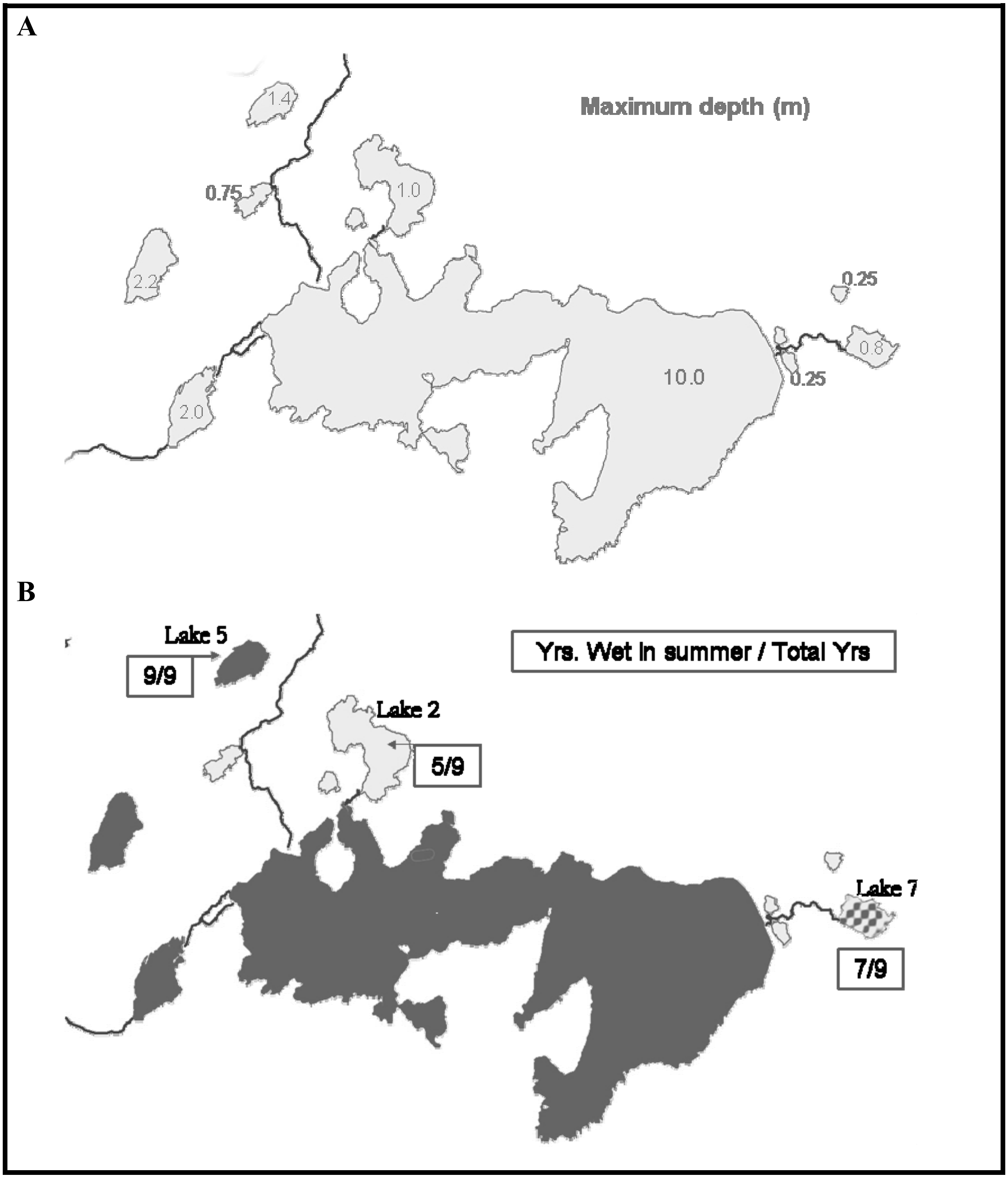

FIGURE 4. (a) Maximum depth of Dusy lakes, Kings Canyon National Park, California, USA, measured at the beginning of summer (i.e., right after snowmelt). Many lakes were very shallow (< 1m), and Lake #1 was noticeably deeper (10 m) than the other lakes. (b) Frequency of summer drying. Shading indicates water availability: dark – permanent year-round water; light shading – summer water only during wet years (boxed ratios indicate the number of years with summer water during the period 1997-2006).

number of times they dried during the 10 years under study. Thus, ranks 1 and 2 were given to permanently wet lakes, ranks 3 and 4 to those lakes that dried up in about half of the years, and rank 5 is given to the lakes that dried every or almost every year. We assigned each lake only one PR for all the years under study.

The second metric that we used to evaluate the end-of-summer lake drying was *drying code* (DC; from 1 to 4). The code reflects the end-of-summer water status in a lake during the previous two years, i.e., during a time when the current generation of *R. sierrae* metamorphs was developing. Thus, DC 1 indicates that the lake remained wet both of the preceding two summers, while the other DC codes indicate that the lake dried up at least once during those two years (DC 2: lake dry two years ago; DC 3: lake dry last year; DC 4: lake dry during both of the two preceding years) . A single lake can thus be assigned more than one DC value depending on its end-of-summer status in each year. We used PR and DC metrics to aggregate the lakes into groups (five groups using PR, and four groups using DC) when analyzing the effect of lake drying on *R. sierrae* recruitment (next section).

Frog surveys.—To document changes in the *R. sierrae* population, we began surveying frogs in the Dusy Basin lakes during June-October 1997; lakes were frozen and frogs inactive in winter months. We counted frogs using visual surveys of each Dusy Basin lake and the connecting streams at approximately bi-weekly intervals. During the survey, a researcher would walk slowly around the perimeter of the lake and thorough the lake in some cases (e.g., Lake 2), recording the numbers of *R. sierrae* without having to handle the animals. We assigned frogs to one of the following four age-classes: egg (visible in egg-masses underwater), larva (tadpoles, underwater), metamorph (a recently metamorphosed frog, small size, may still have had the remnant of tail), and adult (comprising both sub-adults and sexually mature adult individuals). This classification enabled us to estimate recruitment (the transition of individuals into the next-older age class from year to year).

While the *R. sierrae* adults can move overland from lake to lake (Pope and Matthews 2001), the other life stages are completely (eggs, tadpoles) or almost completely (metamorphs) restricted to life in water; thus, *R. sierrae* individuals in these early life stages will usually be found in the same water body where they hatched. We noted that not all lakes in the basin were used by *R. sierrae* for breeding (Fig. 1; Matthews, unpubl. data). Thus, we restricted our statistical analyses to the metamorphs found in the “breeding lakes” (i.e., the lakes where egg masses had been observed). We assumed that these metamorphs were at least in their third year of life and that they had hatched in the lake where we found them (and thus that lake could not have dried up any time during the previous 2.5 years). We base the latter assumption on our observation of very limited connectivity between Dusy Basin water bodies during the summer season (and that the metamorphs are inactive and unlikely to move during the winter months when the lakes are frozen).

To indicate the size of the metamorph age-class each year, we used the within-season maximum recorded number of metamorphs in each lake (“MaxMets”). To evaluate the effect of lake drying on frog recruitment, we tested for differences in MaxMets counts for each year in lakes grouped by PR and DC metrics, using a t-test, and Mann-Whitney U, where assumptions for parametric tests were not met ($\alpha = 0.05$).

Data sets used in the lake drying / survey analyses.—We recorded the end-of-summer water status (Wet/Dry), and mapped the bathymetry and surveyed *R. sierrae* in all 15 lakes in Dusy Basin. Because the lake mapping was started in 2002 (then repeated in 2003, 2005, and 2006), the detailed within-season water decline data (i.e., volume calculations) were only available for those years; whereas, the end-of-season water status (wet/dry) and frog counts were available for all the years 1997-2006 (with the exception of 2004). Therefore, to maximize the information that can be extracted from the data, we used two separate data sets in the above analyses.

First, for the year-to-year water availability analysis (exploring the effects of complete lake drying), we derived the frog population data from all nine “breeding lakes” (the six lakes shown in Fig. 1, and lakes #20, #21 and #22), for all years 1997-2006, except 2004. Second, for the within-year water level analysis, we used bathymetry data and the frog population data from years 2002 and 2003, from two examples that represent the two types of lakes used as primary breeding habitat by *R. sierrae*:

(1) a small shallow lake that has a 50% chance of completely drying during the summer (Lake #2),
(2) a small, but slightly deeper lake, that may lose a significant proportion of its volume during the summer, but has nevertheless retained some water during all of the past nine summers (Lake #5).

RESULTS

Climate effects on lake drying and breeding effort—Lake permanence depended on snowpack and summer rain, and the snowpack depth varied somewhat in Dusy Basin from 1997-2007 (Fig 2). In four of the 10 years, the snowpack exceeded the long-term mean of 88.5 cm SWE, calculated for period 1930-2006 (horizontal bar in Fig. 2). The summer (July-September) rainfall during the study period was also quite variable. The average (1930-2006) summer rainfall at the Lake Sabrina Station

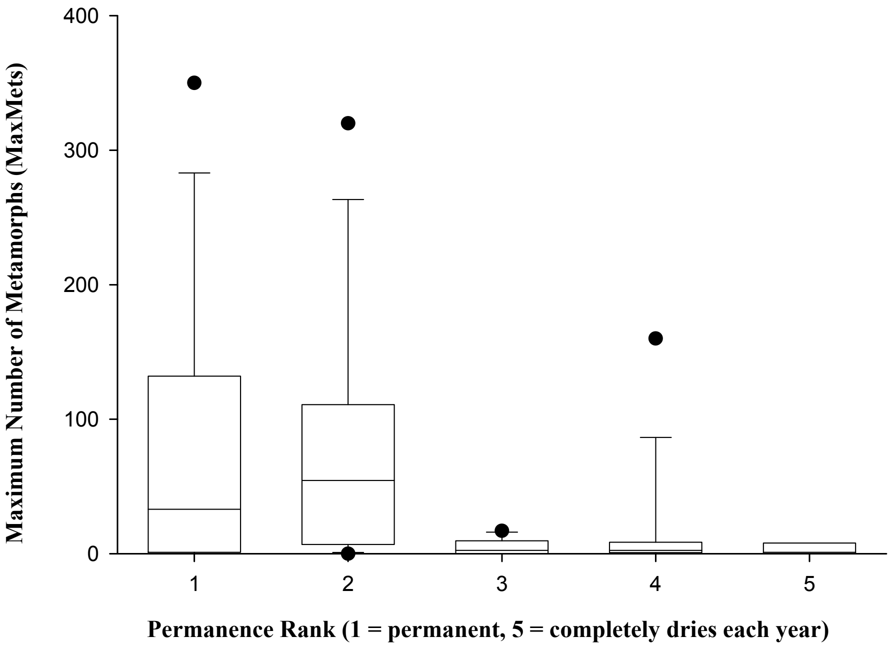

FIGURE 5. The maximum number of metamorphs (MaxMets), an indicator or frog recruitment into older age-classes, in lakes grouped by Permanence Rank (PR), a measure of the drying frequency during the nine years of study.

sensor was 4.6 cm, and the summer precipitation in Dusy Basin was below that long-term average in six out of the last 10 years (Fig. 2), and these were also the years when the snowpack depth was below the long-term mean (with the exception of 2006). In each of those six years, at least one of the lakes used by *R. sierrae* for breeding had dried during the summer months (Fig. 2). Some of the breeding lakes retained water in all summers. During the four years that were characterized by high snowpack, the summer rainfall was also ≥ long-term average (Fig. 2), and none of the breeding lakes experienced summer drying. The breeding effort increased with the yearly snowpack, so that the MaxTadpoles count increased with the rising snowfall up to about 100 cm of SWE, but decreased above that value (Fig. 3; nonparametric fit, $r^2 = 0.1$).

Lake volume mapping and metamorph surveys—*(1) Year-to-year analysis: End-of-summer water status and its influence on* R. sierrae *population.*

The Dusy Basin lakes identified as important *R. sierrae* breeding habitat (Fig. 1) are very shallow, many of them < 1 m deep when full at the beginning of summer (Fig. 4a). Considering the large variation in snowpack (Fig. 2), which is the main source of water, it is not surprising that only two of the small breeding lakes have been observed with permanent year-round water during the nine years of the study (Lakes #4 and #5; Fig. 4b). The other breeding lakes had as much as a 50% chance of drying up during a summer (Lake #2; Fig. 4b).

The yearly highest-observed number of metamorphs (MaxMets) plotted in lakes grouped by Permanence rank (PR; Fig. 5), differed between the lakes that were always wet (ranks 1 and 2) and those that dried at least once during the study (ranks 3, 4, and 5). After aggregating the ranks into those two categories ("always-wet" and "sometimes-dry"), we found there were significantly more *R. sierrae* metamorphs present in the always-wet category (median number of metamorphs = 35 individuals) than in the sometimes-dry category (median: 2 individuals; Mann-Whitney U test, $T = 1283$, $P < 0.001$). However, the MaxMets counts were not significantly different in lakes within each of the two types of categories (i.e., no significant difference in MaxMets between lakes in ranks 1 and 2 [H = 0.258, $P = 0.61$]; no significant differences in MaxMets among lakes ranked 3, 4, and 5[H = 0.870, $P = 0.65$]).

Plotting the MaxMets in lakes grouped by drying code (Fig. 6) revealed that the lakes that retained water during both the previous two summers (DC 1) had significantly more metamorphs than those lakes which dried at least once in the preceding two years (medians: 13.5 individuals for DC 1, and 2 individuals for lakes in combined DCs 2, 3 and 4; Mann-Whitney U test, $T = 338$, $P = 0.001$). The MaxMets count was not significantly different among the categories of lakes that dried (once or twice) during the preceding two years

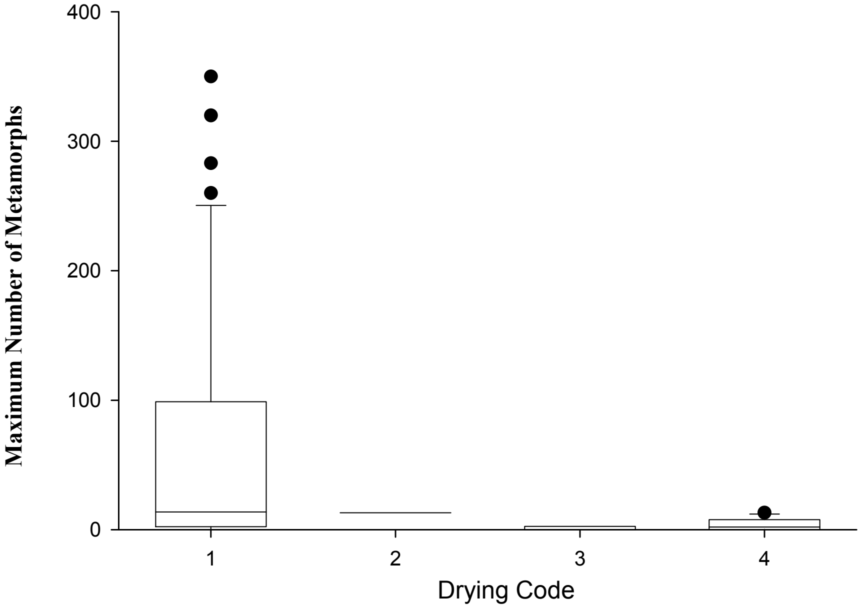

FIGURE 6. MaxMets in lakes grouped by Drying Code (DC), a measure of the lake's drying behavior during the preceding two years. For drying code, 1 = wet last 2 yrs, 2 = wet last yr, 3 = wet 2 yrs ago, 4 = dry last 2 yrs.

(i.e., no significant differences among lakes in DCs 2, 3, and 4).

(2) Within-year water availability: lake level decrease and its effect on R. sierra.—Two differences in the patterns of lake level decrease were observed in the two example lakes (Lakes #2 and #5; Fig. 7 and 8). The first was the effect of lake depth: the slightly deeper lake (#5) retained water in its central (deepest) portion at the end of the summer (Fig. 8, fourth panel), while the shallower Lake #2 dried out completely (Fig. 7, fourth panel). The second noticeable difference in lake drying was observed between a dry year (defined as having both low snowpack and low summer rainfall), 2002, and an average year, 2003. Almost no change in water volume occurred in the average year (compare the bottom two panels of Fig. 7; and those of Fig. 8), in contrast to dramatic changes in a dry year (top four panels in Fig. 7 and 8): 100% volume loss in Lake #2, and 67% volume loss in Lake #5. In contrast, the largest lake in the basin, Lake #1, had retained over 85% of its water at the end of the summer in the dry year, and over 96% during the normal year (data not shown).

Rana sierrae population structure in each lake changed during the summer (Fig. 7 and 8), partially because the adult frogs can move throughout the basin. Noticeably, the dramatic decline in water level in Lake #5 did not affect the metamorph numbers in either 2002 or 2003. The observed increase in metamorph numbers within a single summer is likely caused by the ongoing recruitment during the summer of the 3rd-year tadpoles into the metamorph age class.

DISCUSSION

This is the first study to document the connection between water availability and the population structure of *R. sierrae*, and to use the low-water years to simulate the potential effects of a future warming and drying climate on *R. sierrae* in high-elevation lakes. The importance of dry-summer years (which may become more common in the future because of climate change) is evidenced in the lack of metamorphs in those lakes that had experienced complete drying sometime in the preceding two years. However, such complete mortality was not observed in the lakes that had retained even only a small fraction of their original water. That is, the decline of water level by itself, however dramatic, does not appear to result in tadpole mortality unless the lake dries completely.

The *R. sierrae* population changes in the two contrasting types of lakes are attributable mostly to the end-of-summer water availability. Both the shallower-type lake (#2) and a deeper-type one (#5) are important as breeding habitat. However, the former dried out in late August of 2002, and contained no metamorphs in 2003, unlike the slightly deeper lake (#5), which had declined dramatically but did not dry completely in 2002. The frog survey in Lake #5 illustrates this point in another

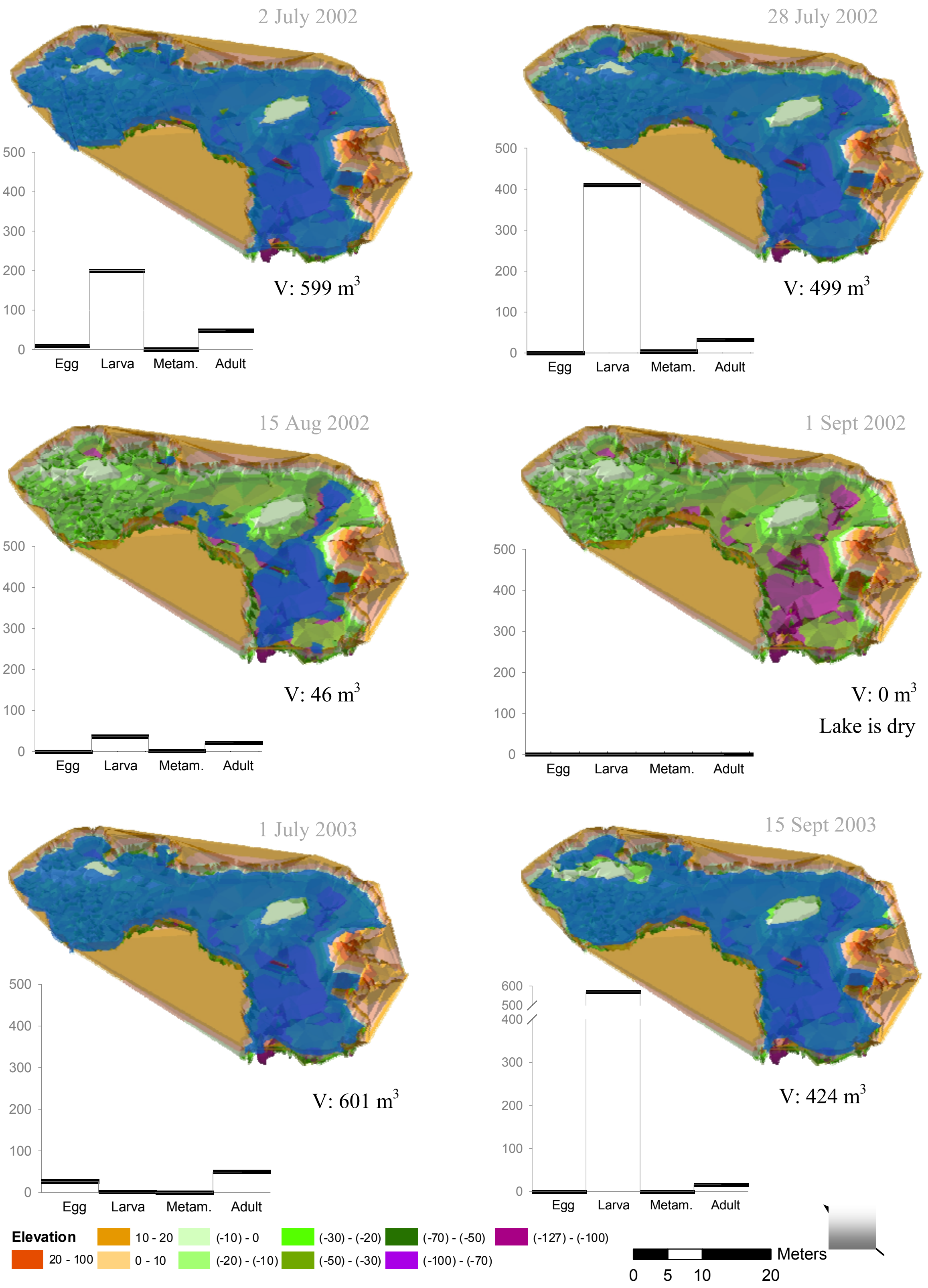

FIGURE 7. Water volume change in Lake #2 in Canyon National Park, California, USA comparing a below-normal snowfall year (2002) and an average snowfall year (2003), and *R. sierrae* survey results (counts of individuals in four age-classes). Volume of water (V) in m^3; water depth (color values) in cm relative to the water surface on 1 July 2002. For 2002 (top four panels), the progression of drying is shown through the dry summer season (June-September); the lake was completely dry by 1 September. For 2003 (bottom two panels), only the beginning and the end of summer season data are shown as water volume changed little during the entire summer. Notice the lack of metamorph age-class in both years (the lake dried up in 1999 and in 2002, and the lack of metamorphs in 2002 possibly reflects that).

way as well: the metamorphs were present here in 2002; whereas, none were seen in Lake #2, (a consequence of the Lake #2 having dried up in 1999). Nevertheless the adult frogs continued to repopulate Lake #2 when it refilled in 2003, and intensive breeding continued as evidenced by high tadpole counts in 2003. Both lakes are suitable habitat for adults, as seen at the end of summer in a normal-precipitation year (2003), and even a greatly reduced lake is acceptable (Lake #5 in August 2002). Thus, while winterkill of the overwintering adults has been documented as a cause of mortality in other amphibians (Bradford 1983; Pilliod and Peterson 2001), we propose the drying-induced summerkill of tadpoles as an additional, and distinct, mortality mechanism, which could become more important in a warmer and drier climate.

Additionally, we found little evidence for winterkill in our study site. If winterkill were the dominant mortality cause, we would expect to find a depressed number of metamorphs in the lakes that declined and then froze to the bottom in winter without drying the previous summer (e.g., Lake #5 in 2002). Furthermore, we would also expect to see similarly low metamorph counts in the lakes that dried up and in those that declined without drying (but then froze in winter). Our results show the opposite pattern: no effect of water level decline without drying, but significant MaxMets differences between the sometimes-dry and the never-dry lakes. This indicates that tadpoles are likely surviving winters in small remnant pools of water, even if severely chilled, as shown by Bradford (1983) for the tadpoles of the closely related *R. muscosa*. Further evidence against the winterkill-mortality in our area is found in survival patterns that became apparent in a 10-year study of PIT-tagged frogs (Matthews and Preisler, unpubl. data). In that study, adult *R. sierrae* had the highest year-to-year survival during the highest snowpack years, indicating that longer winters with more snow do not result in lower survival.

It is further notable that, in Dusy Basin, even the very shallow lakes (e.g., Lakes #8 and #9, both < 0.3 m deep) serve as breeding lakes and as tadpole habitat but, because these lakes dry out almost every year, there is no recruitment into older age classes. That is, presence of *R. sierrae* tadpoles in a lake indicates successful breeding, but this might not result in a viable population in shallow lakes where the recruitment into older age-classes is unsuccessful. This appears to indicate a form of a classic sink habitat (Holt 1985; Pulliam 1988), noted in other studies for other long-lived alpine amphibians that are today restricted to small, fishless lakes (e.g., the Long-toed Salamander, *Ambystoma macrodactylum*; Pilliod and Peterson 2001). The assessment of this effect is difficult because the *R. sierrae* adult counts in each lake fluctuated at least somewhat independently of the water volume, as the frogs moved from breeding to feeding to overwintering sites (Matthews et al. 1999) because of the changing habitat requirements. Some lakes, for example, are more important as overwintering habitat than others (cf. Lakes #2, #5). It is nevertheless apparent from the low breeding effort in Lake #1 that this large permanent lake, despite representing a stable habitat for adults, does not serve as a source (*sensu* Pulliam 1988) at present as not enough frogs breed in the large lake to force movement into the in drying-prone smaller "sink" lakes.

It is less clear, however, to what extent the greater number of egg masses/tadpoles is driven by environmental conditions (e.g., water temperature) and food availability in smaller lakes, and how much it is due to the effects of predatory trout in larger lakes. This is an important distinction as the tadpoles are likely the most vulnerable life stage of *R. sierrae*, because of their long development: even one dry year in every four might be enough to depress recruitment into adult life stages by extirpating up to four year-classes of tadpoles. It is, therefore, unlikely that *R. sierrae* breeding in Dusy Basing was historically restricted to small lakes, as it is today (Knapp and Matthews 2000). The larger lakes likely would have served as breeding refuges prior to the introduction of fish. That is, they would have supported at least some breeding and would allow those tadpoles to survive the dry years, thus ensuring recruitment. An analogous situation, a habitat with both large and small lakes but with amphibians restricted to the latter because the large lakes contained fish, was described in the case of the Long-toed Salamander (Pilliod and Peterson 2001). Similar population-level effects were observed: breeding without recruitment, although, as noted, the main cause of mortality in that ecosystem was reportedly due to winterkill (freezing), and larger lakes would have served as "overwintering refuges" for larval salamanders (Pilliod and Peterson 2001).

In another example, a 16-year study of amphibians inhabiting a temporary pond (Semlitsch et al. 1996) examined the interaction between hydroperiod, breeding, recruitment, competition, and predation. It was found that the hydroperiod was the most important factor, directly influencing both the number of metamorphosing frog larvae and the total number of species. However, Semlitsch et al. (1996) also noted that the effects of these biotic and abiotic factors were difficult to separate in their study system, and that local population dynamics may be influenced also by migration among ponds. Both of those remarks apply quite well to our study site.

Furthermore, in Dusy Basin the local importance of biotic factors (fish predation) and abiotic factors (lake drying) varies both by lake (in large vs. small lakes, respectively) and over time (high-snowpack vs. low-snowpack years). In Dusy Basin, we can thus observe the negative effects on *R. sierrae* occurring at both ends of the "hydroperiod gradient" noted by Semlitsch et al.

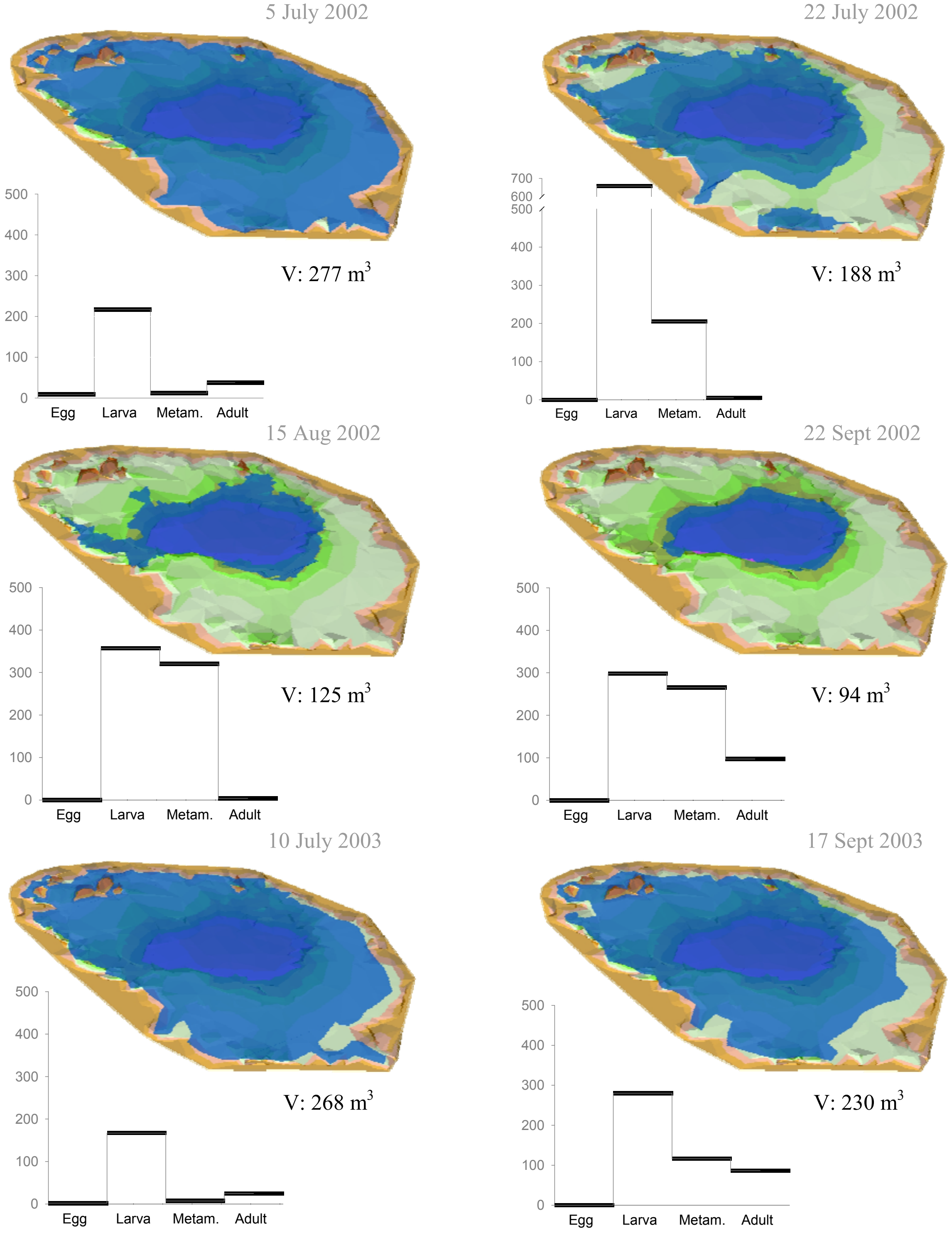

FIGURE 8. Water volume change in Lake #5 in Canyon National Park, California, USA during the summer of 2002 and 2003. The legend is the same as Fig 7. This lake receded dramatically, but did not dry out, during the low-snowpack year (despite having a much smaller volume than Lake #2). Notice the presence of metamorphs both years, possibly indicating that even the small water volume was sufficient to allow tadpole survival (this lake has never been hydrologically connected to other lakes).

(1996): in the large permanent lakes, predation by fish limits frog breeding, and in the small drying-prone ponds, the desiccation prevents successful frog recruitment.

Ironically, it is quite possible that the periodic drying of the small lakes has had a beneficial effect of preventing permanent fish establishment in those lakes. The trout that are now resident in the permanent lakes might have an opportunity to invade a few small lakes during the snowmelt (early summer months) when a few lakes are connected by ephemeral streams, but would then perish along with the tadpoles if the lake dried out. A similar situation was described by Semlitsch et al. (1996), who noted that although the years with short hydroperiods would be "catastrophic for most species," in the following years some amphibians might actually benefit from the elimination of predators (salamander or insect larvae) or competitors.

With the larger lakes now mostly "off limits" to breeding *R. sierrae*, any environmental factor that increases the frequency of summer drying of the small lakes is likely to contribute to further population decline. This is similar to what has been suggested before for amphibians in general (Corn 2005). If the predicted effects of climate change on Sierra Nevada water balance (Knowles and Cayan 2002, 2004) prove correct and the winter snowpack diminishes, the summer drying of small lakes is likely to become more frequent, and frog recruitment less successful. Of additional concern is that this loss of high-snowpack years may also depress egg production, as the highest egg mass counts have been recorded in summers following the high-snowpack years. Thus, climate change is likely to result in a lower breeding success from the combination of drying-induced mortality (lower recruitment) and the loss of the high egg production that is dependent on above-average snowpack (lower fecundity). This and other studies (Bradford 1989; Knapp and Matthews 2000) have demonstrated that an introduced predator (trout) has confined most frog breeding to exactly those lakes that are the most likely to dry out during the summer, and has eliminated a potential refuge of larger lakes during dry years by preventing the breeding there. A conservation strategy should recognize this interaction between the introduced predator and the likely future effects of climate change, and aim to expand the breeding habitat of *R. sierrae* to a greater fraction of the frog's former range, including large, permanent lakes.

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LITERATURE CITED

Blaustein, A.R., and J.M. Kiesecker. 2002. Complexity in conservation: lessons from the global decline of amphibian populations. Ecological Letters 5:597-608.

Blaustein, A.R., T.L. Root, J.M. Kiesecker, L.K. Belden, D.H. Olson, and D.M. Green. 2003. Amphibian breeding and climate change: a reply to Corn. Conservation Biology 17:626-627.

Bradford, D.F. 1983. Winterkill, oxygen relations, and energy-metabolism of a submerged dormant amphibian, *Rana muscosa*. Ecology 64:1171-1183.

Bradford, D.F. 1989. Allotopic distribution of native frogs and introduced fishes in high Sierra Nevada lakes of California - Implication of the negative effect of fish introductions. Copeia 1989:775-778.

Bradford, D.F., F. Tabatabai, and D.M. Graber. 1993. Isolation of remaining populations of the native frog, *Rana muscosa*, by introduced fishes in Sequoia and Kings Canyon National Parks, California. Conservation Biology 7:882-888.

Corn, P.S. 2003. Amphibian breeding and climate change: the importance of snow in the mountains. Conservation Biology 17:622-625

Corn, P.S. 2005. Climate change and amphibians. Animal Biodiversity and Conservation 28:59-67.

Drost, C.A., and G.M. Fellers. 1996. Collapse of a regional frog fauna in the Yosemite area of the California Sierra Nevada, USA. Conservation Biology 10:414-425.

Hastie, T.J., R. Tibshirani and J. Friedman. 2001. The Elements of Statistical Learning: Data Mining, Inference, and Prediction. Springer, New York, USA.

Holt, R.D. 1985. Population dynamics in two-patch environments: some anomalous consequences of an optimal habitat distribution. Theoretical Population Biology 28:181-208.

Knapp, R.A., and K.R. Matthews. 2000. Non-native fish introductions and the decline of the Mountain Yellow-legged Frog from within protected areas. Conservation Biology 14:428-438.

Knowles, N., and D.R. Cayan. 2002. Potential effects of global warming on the Sacramento/San Joaquin watershed and the San Francisco estuary. Geophysical Research Letters 29.

Knowles, N., and D.R. Cayan. 2004. Elevational dependence of projected hydrologic changes in the San Francisco Estuary and watershed. Climatic Change 62:19-336.

Knowles, N., and D.R. Cayan. 2002. Potential effects of global warming on the Sacramento/San Joaquin watershed and the San Francisco estuary. Geophysical Research Letters: 29.

Matthews, K.R., R.A. Knapp, and K.L. Pope. 2002. Garter snake distributions in high-elevation aquatic ecosystems: Is there a link with declining amphibian populations and nonnative trout introductions? Journal of Herpetology 36:16-22.

Pilliod, D.S., and C.R. Peterson. 2001. Local and landscape effects of introduced trout on amphibians in historically fishless watersheds. Ecosystems 4:322-333.

Pope, K.L., and K.R. Matthews. 2001. Movement ecology and seasonal distribution of Mountain Yellow-legged Frogs, *Rana muscosa*, in a high-elevation Sierra Nevada basin. Copeia 2001:787-793.

Pounds, J.A., M.R. Bustamante, L.A. Coloma, J.A. Consuegra, M.P.L. Fogden, P.N. Foster, E. LaMarca, K.L. Masters, A. Merino-Viteri, R. Puschendorf, S.R. Ron, G.A. Sanchez-Azofeifa, C.J. Still, and B.E. Young. 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. Nature 439:161-167.

Pulliam, H.R. 1988. Sources, sinks, and population regulation. The American Naturalist 132:652-661.

Semlitsch, R.D., D.E. Scott, J.H.K Pechmann, and J.W. Gibbons. 1996. Structure and dynamics of an amphibian community: evidence from a 16-year study of a natural pond. Pp. 217-248 *In* Long-term Studies of Vertebrate Communities. Cody, M.L., and J. Smallwood (Eds.). Academic Press, Boston, Massachusetts, USA.

Stuart, S., J.S. Chanson, N.A. Cox, B.E. Young, A.S.L. Rodrigues, D.L. Fishman, and R.W. Waller. 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306:17783-1786.

United States Fish and Wildlife Service (USFWS). 2007. Species Assessment Form for the Mountain yellow-legged frog (U.S.A., all mountain yellow-legged frogs that occur north of the Tehachapi Mountains in the Sierra Nevada). 66 pp. Most recent version available at http://ecos.fws.gov/docs/candforms_pdf/r8/D02H_V02.pdf (last accessed 9. November 2008)

Vredenburg, V.T., R. Bingham, R. Knapp, J.A.T. Morgan, C. Moritz, and D. Wake. 2007. Concordant molecular and phenotypic data delineate new taxonomy and conservation priorities for the endangered Mountain Yellow-legged Frog. Journal of Zoology 271:361-374.

Vredenburg, V.T., G.M. Fellers, and C. Davidson. 2005. Mountain Yellow-legged Frog. (species account). Pp. 563-566 *In* Amphibian Declines, Lannoo, M. (Ed.). University of California Press, Berkeley, California, USA.

Zweifel, R.G. 1955. Ecology, distribution, and systematics of frogs of the *Rana boylii* group. University of California Publications in Zoology 54:207-292.