Assessing Changes in Amphibian Population Dynamics Following Experimental Manipulations of Introduced Fish

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Abstract: *Sport-fish introductions are now recognized as an important cause of amphibian decline, but few researchers have quantified the demographic responses of amphibians to current options in fisheries management designed to minimize effects on sensitive amphibians. Demographic analyses with mark–recapture data allow researchers to assess the relative importance of survival, local recruitment, and migration to changes in population densities. I conducted a 4-year, replicated whole-lake experiment in the Klamath Mountains of northern California (U.S.A.) to quantify changes in population density, survival, population growth rate, and recruitment of the Cascades frog (Rana cascadae) in response to manipulations of non-native fish populations. I compared responses of the frogs in lakes where fish were removed, in lakes in their naturally fish-free state, and in lakes where fish remained that were either stocked annually or no longer being stocked. Within 3 years of fish removals from 3 lakes, frog densities increased by a factor of 13.6. The survival of young adult frogs increased from 59% to 94%, and realized population growth and recruitment rates at the fish-removal lakes were more than twice as high as the rates for fish-free reference lakes and lakes that contained fish. Population growth in the fish-removal lakes was likely due to better on-site recruitment of frogs to later life stages rather than increased immigration. The effects on R. cascadae of suspending stocking were ambiguous and suggested no direct benefit to amphibians. With amphibians declining worldwide, these results show that active restoration can slow or reverse the decline of species affected by fish stocking within a short time frame.*

Keywords: amphibian declines, lake restoration, MARK, mark–recapture, *Rana cascadae*, trout effects

Evaluación de Cambios en la Dinámica Poblacional de Anfibios después de Manipulaciones Experimentales de Peces Introducidos

Resumen: *Las introducciones de peces para la pesca deportiva ya son reconocidas como una causa importante de la declinación de anfibios, pero pocos investigadores han cuantificado las respuestas demográficas de anfibios a las opciones actuales de manejo de pesquerías diseñadas para minimizar efectos sobre anfibios sensibles. Los análisis demográficos con datos de marcaje–recaptura permiten que investigadores evalúen la importancia relativa de la supervivencia, el reclutamiento local y la migración a cambios en las densidades poblacionales. Realicé un experimento de cuatro años, replicado en las Montañas Klamath en el norte de California (E. U. A.) para cuantificar los cambios en la densidad poblacional, supervivencia, tasa de crecimiento poblacional y reclutamiento de ranas (Rana cascadae) en respuesta a manipulaciones de poblaciones de peces no nativas. Comparé las respuestas de las ranas en lagos en los que los peces fueron removidos, en lagos en su estado natural libre de peces y en lagos donde permanecían peces que eran abastecidos anualmente o que ya no eran abastecidos. A tres años de la remoción de peces de 3 lagos, las densidades de ranas incrementaron en un factor de 13.6. La supervivencia de ranas adultas jóvenes incrementó de 59% a 94%, y el crecimiento poblacional realizado y las tasas de reclutamiento en los lagos sin peces fue más del doble que las tasas en los lagos de referencia libres de peces y los que contenían peces. El crecimiento poblacional en los lagos donde*

fueron removidos los peces probablemente se debió a un mejor reclutamiento de ranas en estadios tardíos y no a un incremento de la inmigración. Los efectos de la suspensión del abastecimiento de peces sobre R. cascadae *fueron ambiguos y no sugirieron un beneficio directo para los anfibios. Con la declinación mundial de anfibios, estos resultados muestran que la restauración activa puede desacelerar o revertir la declinación de especies afectadas por el abastecimiento de peces en un período de tiempo corto.*

Palabras Clave: declinaciones de anfibios, efectos de truchas, marcaje-recaptura, MARK, *Rana cascadae*, restauración de lagos

Introduction

Human introductions of species outside their natural ranges now cause almost all biological invasions in which the introduced species have negative effects on resident organisms (Alpert 2006). The worldwide practice of stocking non-native fishes in aquatic systems has well-researched negative consequences for native organisms including fishes (e.g., Bonar et al. 2005; Hasegawa & Maekawa 2006) and amphibians (Kats & Ferrer 2003). Introduced fishes affect native species through competition (Hasegawa & Maekawa 2006; Finlay & Vredenburg 2007), predation (Vredenburg 2004), transmission of disease (Kiesecker et al. 2001), or by disruption of ecosystem processes (Eby et al. 2006). Impacts are often strongest for species that evolved without fish predators (Kats & Ferrer 2003).

In the western United States thousands of historically fishless mountain lakes have been stocked with trout (primarily *Oncorhynchus*, *Salmo*, and *Salvelinus* spp.) since the late 1800s to increase recreational fishing opportunities (Pister 2001). Recently there has been increasing pressure to manage these fisheries to minimize their effects on sensitive native species. For example, a recent California Superior Court ruling found that the California Department of Fish and Game (CDFG) must consider the effects of fish stocking on sensitive aquatic species when making future stocking decisions (*Pacific Rivers Council Center for Biological Diversity v. California Department of Fish and Game* 2007).

Although stocking non-native trout in mountain lakes continues, it recently has been greatly reduced in some regions where sensitive amphibians occur, including the mountain yellow-legged frog (*Rana muscosa*) and Cascades frog (*R. cascadae*). Benefits of stocking cessation are unclear because fish populations may persist in a high proportion of lakes through local recruitment. About 70% of alpine lakes in the Sierra Nevada, California, support reproducing trout populations, and short-term suspension of stocking (approximately 5 years) does not result in significant changes in fish density (Armstrong & Knapp 2004). Nevertheless, following a long-term hiatus in fish stocking (>20 years) in Sierra Nevada national parks, frog populations are more common and have higher densities compared with neighboring national forest lands,

where stocking continues (Knapp & Matthews 2000). Some management agencies have begun active restoration programs to remove introduced fishes from specific mountain lakes (Knapp et al. 2007). The increased occurrence and size of amphibian populations following fish removals (Vredenburg 2004; Knapp et al. 2007; Walston & Mullin 2007) is strong evidence that removal of fishes can benefit sensitive amphibians.

A more thorough understanding of the relationship between introduced fishes and amphibians can be gained with a rigorous assessment of population-level responses of amphibians to fish removals and stocking cessation. Given that fluctations in population size result directly from changes in demographic variables, it is important to consider the mechanisms underlying any numerical patterns observed (Krebbs 1996). For example, populations can grow due to better recruitment to later life stages, better retention of individuals, or increased immigration. Using demographic analyses, researchers can determine the relative importance of these factors. This is especially important given the imprecise nature of large-scale experiments (May 1999), such as whole-lake fish manipulations, and the potentially confounding factors of other stressors to amphibians. There is strong evidence that disease (Berger et al. 1998; Pieter 2006), chemical contaminants (Hayes et al. 2006), and climate change (Pounds et al. 1999; Araujo et al. 2006) can cause significant declines in amphibian populations in protected mountain habitats either independently or synergistically (Blaustein et al. 2003; Pounds et al. 2006). Quantifying the demographic response of amphibians to changes in fish populations can (1) help validate and explain the observed population results, (2) help distinguish between changes caused by fishes versus other stressors, and (3) be used to generate estimates of parameters for simulation models. Yet, to date, no researchers have tested the influence of introduced fishes on the dynamics of native frog populations through their influences on demographic variables.

I conducted a 4-year, large-scale, replicated experiment in the Klamath Mountains of northern California (U.S.A.) to test the role of introduced fishes in altering population size and demographic variables of *R. cascadae*, a sensitive amphibian in California whose distribution is negatively associated with introduced trout (Welsh et al. 2006). *R. cascadae* ranges from the Olympic Mountains

in Washington, through the Cascade Mountains from Washington to northern California, and into the Klamath-Siskiyou Mountains of California (Pearl & Adams 2005). I compared changes in density and vital rates of *R. cascadae* in lakes where fishes were removed, lakes that remained in their naturally fish-free state, lakes that were stocked annually, and lakes where stocking was suspended. I specifically tested the following 2 predictions: (1) owing to increased survival and recruitment, densities of *R. cascadae* will be higher in lakes where non-native trout have been removed than in lakes that contain trout, and (2) densities of *R. cascadae* in lakes where stocking has ceased will increase only if densities of the trout population decrease significantly.

Methods

Study Area and Design

The study was conducted from 2003 to 2006 in the Trinity Alps Wilderness, a federally designated wilderness area established in 1984, in the Klamath-Siskiyou Mountains of northern California. In this region steep canyon gradients prevent colonization by fishes into lakes higher than about 1500 m elevation (Welsh et al. 2006). Beginning in the 1800s, trout were introduced to the mountain lakes, and stocking continues today. Approximately 90% of lakes in the region now support non-native trout populations (Welsh et al. 2006).

I selected 16 lake basins distributed throughout the eastern half of the wilderness for the study. Twelve lakes supported introduced trout and 4 were fishless. Selected basins had relatively low recreational use, were relatively small, and were headwater lakes without fishes upstream. Lakes were between 1896 and 2210 m in elevation, ranged from 0.3 to 1.98 ha, and were between 2.4 and 15.3 m deep within mixed conifer to subalpine habitat zones. All lakes supported or were within 1 km of habitat that supported *R. cascadae*, ensuring that amphibian population recovery was possible within the project period. Although I tried to match the physical parameters of the lakes, on average the fish-free reference sites were smaller (mean [SE] = 0.64 ha [0.2]) and shallower (2.67 m [0.15]) than the fish-containing lakes (1.16 ha [0.15] and 5.02 m [0.31], respectively). The 2 largest fish-free reference lakes had been stocked historically (Found Lake was last stocked in 1964 and Shimmy Lake was stocked through the 1990s [B. Aguilar, personal communication]) but neither lake supported self-sustaining fish populations. Ideally, I would have selected historically unstocked lakes; however, there were few such sites and all were small and shallow. Given that fauna in mountain lakes seem to have high resilience (Knapp et al. 2001), I chose sites more similar in physical characteristics even though they had a history of stocking.

I blocked the 16 study lakes into 4 groups of 4 lakes on the basis of geographic location. The 12 fish-containing lakes were then randomly assigned as fish-removal lakes, stocking-suspension lakes, or continue-to-stock lakes. These are the fisheries management options currently being considered by the CDFG for maintaining both a recreational fishery and sensitive amphibian populations in wilderness lakes. The 12 fish-containing lakes had been stocked by the CDFG with brook trout (*Salvelinus fontinalis*), rainbow trout (*Oncorhynchus mykiss*), or both, and CDFG records show that the lakes had supported fish populations for more than 30 years prior to the start of the study (CDFG, unpublished data). I surveyed all lakes during the summer of 2003 prior to implementing the fish treatments. The CDFG maintained fish treatments throughout the study by stocking the stocked lakes yearly with rainbow trout and withholding stocking from the stocking-suspension and removal lakes.

Surveys

Following the pretreatment surveys in summer 2003, crews removed trout from the 4 removal lakes in fall and winter of 2003 and spring of 2004 with multiple, repeated sets of gill nets (Knapp & Matthews 1998). The 36-m-long, 1.8-m-tall sinking monofilament gill nets had 6 panels of different mesh sizes (10, 12.5, 18.5, 25, 33, and 38 mm) and were set perpendicular to shore with float tubes. This technique does not affect nontarget organisms such as frogs or macroinvertebrates (Knapp & Matthews 1998); however, we did catch 11 Pacific giant salamanders (*Dicamptodon tenebrosus*) in the nets during fish removals at one of the fish-removal lakes. Post-treatment sampling was conducted in the summers of 2004–2006. Over the course of a field season (June–September with start date dependent on spring thaw), the 16 study lakes were surveyed every 2 weeks. Six survey trips were conducted during both summers of 2004 and 2005, and 5 were conducted in 2003 and 2006.

Two survey techniques were used on every trip to monitor *R. cascadae* populations at the study lakes: visual encounter surveys (VES; Crump & Scott 1994), to obtain counts of each life stage (egg masses, larvae, subadult and adult frogs) for density comparisons, and capture–mark–recapture (CMR) surveys, to obtain population demographic information on adult frogs. During VES surveys, crews counted all life stages of *R. cascadae* in the lake by searching the shoreline and littoral habitats and by looking under banks and logs and in the littoral zone substrate. During CMR surveys, the lakes and adjacent streams, ponds, and wet meadows were systematically searched for *R. cascadae*. Frogs were captured by hand or net and checked to see if they had been tagged previously. Untagged individuals >42 mm snout–urostyle length (SUL) were marked with passive integrated transponders (PIT tags) following methodology

described by Pope and Matthews (2001). Crews recorded location, PIT tag number, date, sex, weight, and SUL for each frog captured. Surveys were conducted during the warmest part of the day (between 10:00 and 18:00), when frogs were most likely to be basking in the open and larvae would be visible in the warm shallow water (Welsh et al. 2006).

During the mid-July survey of each year, crews also set one gill net per lake for approximately 4 hours to obtain a yearly estimate of trout density (number of fish captured per net hour). A linear regression comparing the number of fish caught per net hour at the fish-removal lakes in 2003 with the actual density of fish removed from the 4 fish-removal lakes showed that catch per net hour and density were highly correlated ($r^2 = 0.95$, $p < 0.01$).

Analytic Methods

DENSITY COMPARISONS

I first compared 2003 pretreatment trout and *R. cascadae* (number of frogs per 100 m of shoreline) densities in the 12 fish-containing lakes with one-way analysis of variance (ANOVA) to ensure that pretreatment values were not significantly different among treatment categories. In 2006 brook trout (*S. fontinalis*) fry were found in Echo Lake, a removal lake, during visual surveys. Because trout removal failed at this site, I removed the Block 4 lakes from the rest of the analyses to maintain the balanced design. I tested for an overall treatment effect on VES-estimated densities of both frogs (subadult and adult combined) and larvae with multivariate analysis of variance (MANOVA). Both densities of frogs and larvae were log-transformed (mean + 1) to normalize distributions. I ran separate univariate repeated measures ANOVAs to test for specific treatment and treatment-by-year effects on the yearly mean densities of frogs and larvae. In the repeated measures analysis, treatment was the between-subjects fixed effect and lake was the within-subjects effect. All analyses used Type III sums of squares. I used Tukey-Kramer multiple comparisons to test for all pair-wise differences between means for treatments and years.

POPULATION MODELING

To compare survival, population growth rate, and recruitment among treatments, I used the CMR data to parameterize Cormack Jolly-Seber (CJS) and Pradel's reverse time population models. Because results showed no differences between stocked and stocking-suspension lakes in the ANOVAs on densities of fish and frogs, I combined the 2 fish treatments into a general "fish containing" category for population analyses. I summarized capture histories for each marked frog by year to indicate whether an animal had been captured at least once or not during each summer sampling season. I then combined the

individual capture histories from each lake into the 3 treatment groups: fish-free reference, removal, and fish containing. I used the data on capture history to build a CJS time-dependent population model in program MARK (White & Burnham 1999). For these models, Φ is apparent survival, p is probability of capture, g is treatment group, and t is time (survey year).

I subjected the general CJS model, $\Phi (g \times t) p (g \times t)$, to goodness-of-fit tests in the program RELEASE (Burnham et al. 1987). In addition to the general goodness-of-fit test, the test component TEST3.SR tests the CJS assumption that all marked animals alive at time i have the same probability of surviving to $i + 1$ (Lebreton et al. 1992). The TEST3.SR provided evidence for the reference and fish removal lakes that previously captured animals had different survival rates than animals captured for the first time, so I included an age-structured CJS model (Lebreton et al. 1992) to account for potential differential survival of the frogs.

Using the TEST3.SR results for insight, I developed a treatment-specific set of models to estimate Φ and p for each treatment group and over time. To correct for model lack of fit, I calculated a variance inflation factor for the general model in MARK with the median $\hat{c}$ approach applied to a quasi-likelihood adjustment (qAIC) for parameter estimation and model selection (Burnham & Anderson 2002). During the project period, environmental conditions were similar and techniques of frog capture remained the same, so capture rates did not seem to vary substantially among years or treatments. I therefore focused my candidate model set on differences in survival rates among treatment groups and over time while holding the recapture rates constant. I considered main effects and interactive and additive effects of treatment and time on survival rates. I used differences in qAIC values (ΔqAIC) for model comparison and qAIC weights to identify the most parsimonious model from the candidate model set (Burnham & Anderson 2002). The most parsimonious model was subjected to a bootstrap goodness-of-fit test with 1000 simulations to ensure that the model deviance fell within the distribution of deviances of the simulated data.

To investigate differences in population growth rates (λ) and recruitment (γ) of adult frogs (>42 mm SUL) among the treatment groups and over time, I used a Pradel's reverse-time model (Pradel 1996). The λ estimated from Pradel's models is the realized growth rate of the age class of the marked animals and is not equivalent to the growth rate of the population as a whole. Recruitment is estimated by subtracting the expected number of survivors from time i to $i + 1$ from the actual population size at $i + 1$ (Pradel 1996). The recruits are animals not in the adult population at time i, enter the population between i and $i + 1$, and are in the population at $i + 1$ as a result of either growing large enough or immigrating into the population (Nichols et al. 2000). I again used qAIC

for parameter estimation and model selection. Treatment and temporal variation in λ was examined as described for the CJS models, but Pradel's models do not allow for an age effect (Franklin 2001). I selected the Pradel's models with the best model structure for survival from the CJS models that did not include an age effect. I estimated population parameters with model averaging to account for uncertainty in model selection (Buckland et al. 1997).

Results

Density Comparisons

The 2003 pretreatment trout and *R. cascadae* densities were similar among the 12 treatment lakes ($F_{2,9} = 0.6$, $p = 0.57$ and $F_{2,9} = 0.82$, $p = 0.47$, respectively). Starting in the fall of 2003, 626 trout (93% *S. fontinalis* and 7% *O. mykiss*) were removed from the 3 successful fish-removal lakes. Trout were not caught again at these lakes during the 2004–2006 mid-summer 4-hour sets of gill nets. Trout densities showed a decreasing trend at the stocking-suspension lakes and an increasing trend at the stocked lakes from 2003 to 2006 (Fig. 1a), although densities were not significantly different between treatments across years ($F_3 = 1.31$, $p = 0.32$). Two stocking-suspension lakes that had relatively high densities of trout in 2003 showed consistently decreasing densities each following year, whereas one stocking-suspension lake maintained relatively consistent low densities of trout across years.

Fish removals dramatically increased densities of Cascades frogs, in contrast to continued low densities of frogs at the stocked and stocking-suspension lakes (Fig. 1b). There was a significant treatment effect when I compared the densities of both frogs and larvae across treatments (Table 1). In addition, I found a strong treatment-by-year ($p = 0.02$) effect on frog density (Table 1). Posttreatment (2004–2006) frog densities at the removal lakes were greater than all years' densities at both the stocked and stocking-suspension lakes. By 2006 frog densities at the fish-removal lakes were not significantly different from those at the reference lakes. Stocked and stocking-suspension lakes had lower densities of larvae for all years compared with the reference lakes, and although removal lakes were not significantly different from either the reference or fish-containing treatments (likely due to high variance among lakes), they showed a trend toward an increase in density (Table 1; Fig. 1c).

Capture–Mark–Recapture

Between 2003 and 2006, 546 frogs were individually PIT tagged at the fish-free reference lakes, 321 were tagged at the fish-removal lakes, 110 at the stocked lakes, and 79 at the stocking-suspension lakes. The number of
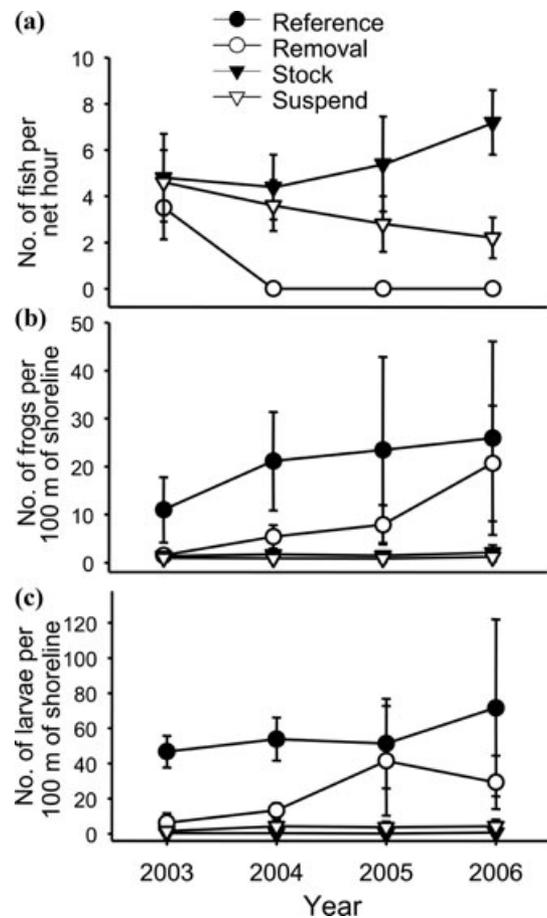

Figure 1. Mean catch rate and SE of (a) non-native trout for the fish-removal lakes, stocked lakes, and stocking-suspension lakes and annual density (mean [SE]) of (b) Rana cascadae *frogs and (c) larvae in fish-free reference lakes and fish treatment lakes for all study years. Three study lakes are included in each treatment and reference category. Fish removal in the removal lakes began in the fall of 2003 following the 2003 surveys.*

untagged adult *R. cascadae* (>42 mm SUL) caught at the fish-removal lakes increased yearly, reaching a 10-fold increase from the 2003 pretreatment year by 2006, whereas the number of untagged adults caught at the reference, stocked, and stocking-suspension lakes remained relatively constant across pre- and post-treatment years (Fig. 2).

Annual survival rates varied by treatment group, according to the most strongly supported models from the age-specific CJS analysis (Table 2, models 1–5). Most of these models also differentiated between frogs in their first interval following release compared with frogs tagged for longer than 1 year (Table 2, models 1, 2, 4, and 5). Newly tagged frogs were smaller than frogs tagged for longer than 1 year (Fig. 3). In addition, newly tagged and previously tagged frogs were significantly larger at the

Table 1. Analysis of variance results assessing the effects of the fish treatment[a] and year on density of *Rana cascadae*.

Source	df	SS[b]	MSE[c]	F	p
MANOVA					
treatment (*T*)	6, 86			13.89	<0.001
ANOVA, frogs					
treatment	3	5.59	1.87	3.52	0.07
lake (*L*)	8	4.23	0.53		
year (*Y*)	3	0.40	0.13	5.48	0.005
$T \times Y$	9	0.61	0.07	2.80	0.02
$L \times Y$	24	0.58	0.02		
ANOVA, larvae					
treatment	3	18.4	6.17	9.22	0.005
lake	8	5.34	0.67		
year	3	0.29	0.10	1.81	0.17
$T \times Y$	9	0.61	0.07	1.25	0.3
$L \times Y$	24	1.30	0.05		

[a]*Treatments include fish removal, stocked annually, and stocking suspension and were compared with fish-free reference lakes.*
[b]*Sum of squares.*
[c]*Mean square error.*

fish-containing lakes compared with the same categories of frogs at the reference and fish-removal lakes (Fig. 3).

Fish removal greatly enhanced the probability of frog survival, according to the CJS model with the lowest qAIC$_c$ (Table 2, model 1). This model ranked substantially better than the others in the set of 13 models (qAIC weight = 0.72, Table 2), so I used this model (and not model averaging) to derive parameter estimates. The bootstrap goodness-of-fit test revealed that the deviance
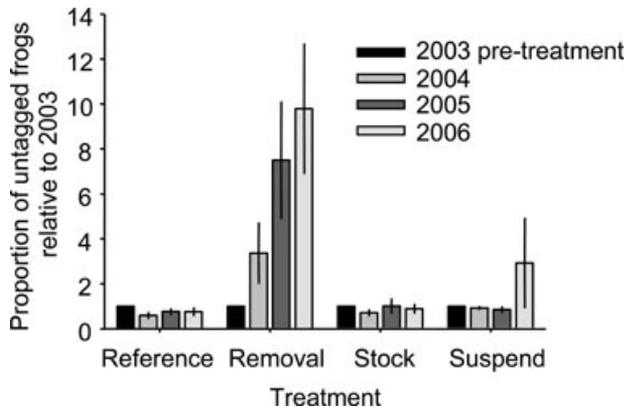

Figure 2. Average yearly change from 2003 in the number of untagged Rana cascadae *frogs >42 mm caught at the reference and treatment lakes (removal, stock, suspend [suspension of stocking]). For each lake, the total number of untagged frogs per year was divided by the total number of untagged frogs caught in 2003 (bars, average proportion of untagged frogs for lakes in each treatment category; lines, SE). For all treatments, 2003 values equal one (number of untagged frogs in 2003/ number of untagged frogs in 2003).*

of the best model fell well within expected values ($p = 0.809$). The model included treatment-by-time variation in age-related survival for the reference and removal lakes but not for the fish-containing lakes. Survival to 2004 of frogs tagged during the 2003 pretreatment year was estimated to be 34% lower at the fish-removal lakes than the reference lakes (Fig. 4a). Nevertheless, by 2006 survival estimates of frogs tagged in 2005 at the removal lakes were 47% higher than survival estimates of frogs tagged during the same period at the reference lakes and 31% higher than the overall estimated survival rate of frogs at the fish-containing lakes (Fig. 4a). The survival rates of frogs that were tagged at least 2 years prior to recapture were not significantly different at the fish removal lakes (0.86; 95% CI 0.54–0.97) compared with the reference lakes (0.74; 95% CI 0.66–0.80) or the fish-containing lakes (Fig. 4b). The estimated recapture probability for all years and all treatments was 0.73 (95% CI 0.67–0.78).

The goodness-of-fit test statistic for the general CJS population model showed significant overdispersion ($X^2_{12} = 22.7$, $p = 0.03$), so I calculated a variance-inflation factor of 1.22 and used it to estimate qAIC for model selection. I included the general CJS model (model 13, Table 2) in the age-specific CJS candidate model set as a reference, and model-selection statistics ranked it the worst of the candidate models with an qAIC weight of <0.01.

Estimates of λ were consistently higher at the fish-removal lakes (range = 1.7 to 3.0) compared with the fish-free reference lakes (range = 1.2 to 1.4) and the fish-containing lakes (range = 0.9 to 1.2, Fig. 4c) on the basis of model averaging (Table 3). Recruitment estimates were also higher at the fish removal lakes (range = 0.8 to 1.8) than at the fish-free reference lakes (range 0.4 to 0.6) and fish-containing lakes (range 0.2 to 0.5, Fig. 4d). Overall, the realized rate of population growth of adult frogs was highly correlated with recruitment rate ($r_p = 0.99$, $n = 9$, $p < 0.001$), but not with adult survival ($r_p = 0.34$, $n = 9$, $p = 0.36$). The most parsimonious model tested indicated a treatment-by-time effect on λ (Table 3, model 1). A bootstrap goodness-of-fit test revealed that the model fit the data adequately with a $p = 0.07$; however, the low p value suggested some evidence of lack of fit, likely due to the inability to include age structure in the model.

Discussion

Frog survival, realized rates of population growth, and recruitment in headwater mountain lakes were strongly increased by eliminating introduced trout. Densities of frogs at the trout-removal lakes were greater than at lakes containing trout within 1 year following trout removals, and densities of frogs became indistinguishable from fish-free reference sites within 3 years following trout removals. This experiment rigorously quantified the

Table 2. Age-structured Cormack–Jolly–Seber models comparing the effects of treatment (fish removal, fish containing) and temporal variation on age-specific apparent survival (Φ) for *Rana cascadae* frogs (>42 mm snout-urostyle length).

Model no.	Model description[a]	qAIC$_c$[b]	ΔqAIC$_c$[c]	qAIC$_c$ weight[d]	Model likelihood	No. of parameters	Deviance
1	{Φ(g*a2-t/t,Fc),p(.)}	1621.77	0	0.718	1.000	12	14.46
2	{Φ(g*a2-t/cFc),p(.)}	1626.25	4.48	0.077	0.107	10	23.02
3	{Φ(g) p(.)}	1626.76	4.99	0.059	0.082	4	35.69
4	{Φ(g*a2-c/t,Fc),p(.)}	1626.96	5.19	0.054	0.075	8	27.80
5	{Φ(g*a2-t/t),p(.)}	1628.07	6.3	0.031	0.043	16	12.56
6	{Φ(t) p(.)}	1628.69	6.92	0.023	0.032	4	37.61
7	{Φ(g*a2-c/t),p(.)}	1630.37	8.6	0.010	0.014	10	27.14
8	{Φ(g+t)p(.)}	1630.46	8.69	0.009	0.013	6	35.35
9	{Φ(g*a2-c/c,Fc),p(.)}	1630.77	9	0.008	0.011	6	35.66
10	{Φ(g*a2-t/c),p(.)}	1631.20	9.43	0.006	0.009	13	21.85
11	{Φ(g*a2-c/c)p(.)}	1632.66	10.89	0.003	0.004	7	35.53
12	{Φ(g*t)p(.)}	1632.97	11.2	0.003	0.004	10	29.74
13	{Φ(g*t)p(g*t)}	1637.49	15.72	0.000	0.000	15	24.04

[a]*Variables: survival, Φ, is modeled as differing by treatment group but otherwise constant over time (g); as differing by capture time only (t); as differing by treatment group and time (g*t); as differing by treatment group and between the first interval following release (age effect) versus all subsequent releases (g*a2), and as differing by treatment group and between the first interval following release versus all subsequent releases for the reference and removal lakes but keeping age class constant for fish-containing lakes (Fc). When survival includes 2 age classes (a2), survival of the first interval class can vary over time (a2-t/.) or remain constant over time (a2-c/.) as can the second age class (a2-./t or a2-./c). Probability of capture is held constant [p(.)] or is modeled as differing by treatment group and time (g*t).*
[b]*Quasi-likelihood adjustment corrected for small sample sizes.*
[c]*qAIC$_{ci}$ − qAIC$_{cmin}$.*
[d]*Weight of evidence that model i is the best model of the set of models tested.*

population-level recovery of *R. cascadae* following fish removals and provided strong direct evidence that fish stocking negatively affects *R. cascadae*. The results also strengthen and expand on recent findings (Vredenburg 2004; Knapp et al. 2007) that show fish removals are a viable option for restoring declining frog populations in mountain lakes of the western United States.

The population growth rate of adult *R. cascadae* was highly correlated with recruitment and not with adult survival, which suggests that initial population growth at the fish removal lakes was primarily due to new frogs entering the adult population instead of increased survival of resident adults. Better recruitment rates could be due to an increase of young frogs within the population surviving to adulthood or an increase in immigrants. On the basis of the small size of the untagged frogs found each year following fish removals and the relative isolation of the headwater study lakes, the increased recruitment at the fish removal sites was likely due to increased survival of larval and juvenile frog stages within the population. Because *R. cascadae* metamorphose in one season (Pearl & Adams 2005) and grow more rapidly in lower-elevation mixed conifer/subalpine habitats compared with alpine species, such as *R. muscosa* (Vredenburg et al. 2005), increased recruitment to the adult life stage could happen quickly if survival of larvae and postmetamorphic frogs increased substantially.

A trend of increasing larval abundance was also evident at the fish removal lakes in the first 2 years following fish removals. This increase was probably due to an increase

in larval survival and not an increase in the number of eggs because no increase in the number of egg masses was observed during this period (K.L.P., unpublished data). This finding suggests that rapid recovery of frog populations is feasible even without a large source population (Vredenburg 2004; Knapp et al. 2005) if a small number of breeding-age frogs occur in the area. In this study I ensured that *R. cascadae* recovery was possible at all sites by selecting sites with co-occurrence of trout and frogs or some frogs nearby, even in very low densities. The 3 restoration lakes I analyzed did not have any large source populations within 2 km.

Although recruitment rates at the restoration lakes were extremely high in the first 2 years following fish removals, they decreased in 2006 to levels close to those at the reference sites. There could be several possible mechanisms for this trend that future monitoring will help elucidate. Two main hypotheses include (1) the recovery of aquatic insect predators at the fish removal lakes increased predation rates on young frogs, and (2) intraspecific competition for space and resources increased as population density increased so that young frogs had more difficulty surviving or remaining on site. Because introduced trout reduce the abundance of predatory macroinvertebrates in mountain lakes (Carlisle & Hawkins 1998; Knapp et al. 2001), there were likely fewer aquatic predators of larval and metamorphosing frogs in the first years following fish removals. Nevertheless by 2006, aquatic insect predators recovered substantially in the fish removal lakes (K.L.P., unpublished data).
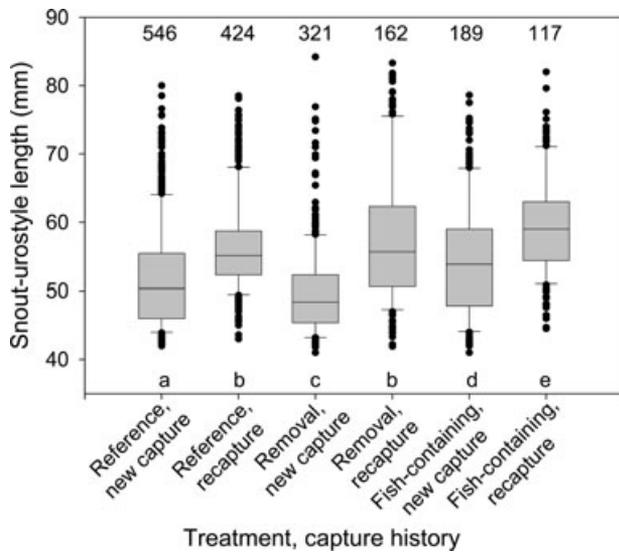
Figure 3. The snout–urostyle lengths of adult Rana cascadae *frogs differentiated by whether they were newly captured or recaptured from the fish-free reference lakes, fish-removal lakes, or fish-containing lakes (horizontal lines, median; bottom and top of bars, 25th and 75th percentiles respectively; whiskers, below and above bars, 10th and 90th percentiles, respectively; dots, points outside the 10th and 90th percentiles; numbers above bars, sample size). Letters (a–e) that differ among bars show statistically significant differences in lengths of frogs among treatment and capture categories at the* $p < 0.05$ *level with a Bonferroni correction for multiple tests (Kruskal–Wallis one-way analysis of variance on ranks followed by Kruskal–Wallis multiple comparison tests with a Bonferroni adjustment).*

By 2006 densities of frogs equaled those at the reference lakes, so density-dependent forces also may have started influencing recruitment levels. Knapp et al. (2007) found evidence of a density-dependent response in *R. muscosa* after several years of rapid population growth following trout removals. They also found large numbers of emigrating frogs from their fish-removal lakes that subsequently colonized additional nearby habitats.

Although population densities were low at the fish-containing lakes, frogs were larger than at the reference or fish removal lakes. Top-heavy age structures indicate insufficient recruitment and declining populations (Alexander 1958; Browne & Hecnar 2007). The high predation pressure of trout on the small size classes of frogs in lakes with fish likely resulted in a dearth of young, small frogs recruiting into the adult population. Nevertheless, I did find that adult frog survival at the fish-containing lakes was comparable to the reference lakes. Large frogs likely have the best chance of survival in lakes with fish because they are too big to fit in the mouths of most trout. Greater predation pressure on small versus large frogs is
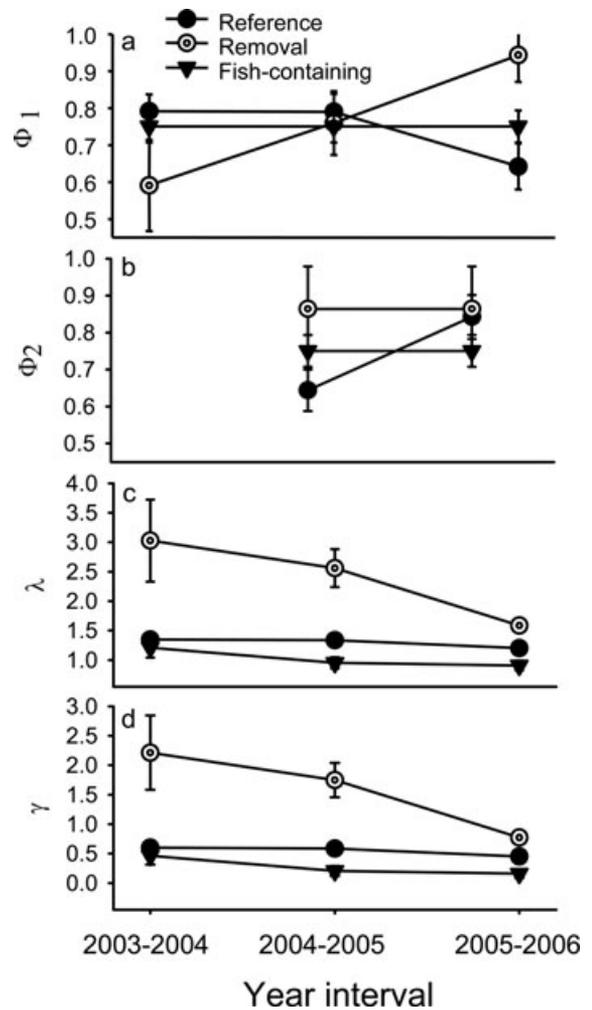

Figure 4. Annual variation (mean [SE]) and SE in survival rates for Rana cascade *in the (a) first interval following PIT tagging and (b) second or third intervals following tagging as estimated from model 1 in Table 2. Estimated yearly (mean [SE]) (c) population growth rate of the adult (>42 mm snout–urostyle length) segment of the population and (d) recruitment rates into the adult population as calculated from model 1 in Table 3.*

likely the reason for the consistent pattern of finding low numbers of adult frogs in lakes where frogs co-occur with trout (e.g., Welsh et al. 2006).

Restoration Implications

Removal of trout from headwater lakes in the Klamath Mountains resulted in rapid recovery of *R. cascadae*. Understanding mechanisms of recovery can provide insights into the nature of the relationship between fishes and amphibians, which could then help managers determine characteristics of amphibian populations best suited for restoration. For example, population models showed that adult *R. cascadae* population growth rates were highest

Table 3. Pradel's reverse-time models to compare the effects of treatment (fish-removal, fish-containing) and temporal variation on the growth rate (λ) of *Rana cascadae* frogs (>42 mm snout–urostyle length).

Model. no.	Model[a] description	$qAIC_c$[b]	$\Delta qAIC_c$[c]	$qAIC_c$ weight[d]	Model likelihood	No. of parameters	Deviance
1	$\{\Phi(g)p(.)\lambda(g^*t)\}$	4119.01	0	0.688	1.000	13	35.69
2	$\{\Phi(g)p(.)\lambda(g+t)\}$	4120.62	1.61	0.308	0.447	9	45.40
3	$\{\Phi(g)p(.)\lambda(g)\}$	4129.40	10.39	0.004	0.006	7	58.22
4	$\{\Phi(g)p(.)\lambda(t)\}$	4224.90	105.89	0.000	0.000	7	153.72
5	$\{\Phi(g)p(.)\lambda(.)\}$	4228.15	109.14	0.000	0.000	5	160.99

[a]*Variables: survival, Φ, is modeled as differing by treatment group but otherwise is held constant over time (g); probability of capture is held constant [p(.)]; and population growth rate, λ, is modeled as differing by treatment group and time (g*t), by treatment group and varying in parallel over time (g+t), by treatment group only (g), by capture time only (t), or as held constant by group and time (.).*
[b]*Quasi-likelihood adjustment corrected for small sample sizes.*
[c]*$qAIC_{ci} - qAIC_{c\,min}$.*
[d]*Weight of evidence that model i is the best model of the set of models tested.*

($\lambda > 3$) immediately following trout eradication and that these rates were closely tied to recruitment rates. Choosing sites with at least some breeding-aged frogs onsite or in adjacent habitats, therefore, seems important for rapid recovery. Nevertheless, it is not necessary to choose sites with large source populations nearby because it appears high recruitment rates can be attained even from small source populations. This is likely because *R. cascadae* has a high reproductive output with about 300–500 eggs/egg mass (Pearl & Adams 2005); a similar response might not be expected from species with low reproductive outputs.

Given the increasing pressure to manage fisheries in wilderness areas to improve conditions for sensitive native amphibians, it is important to understand the effects of changes in fish management on the recovery of amphibians. In California the CDFG has temporarily suspended stocking trout into most lakes where surveys reveal the presence of *R. muscosa* or *R. cascadae*. Existing fish populations may decline naturally because of a lack of spawning habitat or freezing winter temperatures, but they also may remain self-sustaining (Armstrong & Knapp 2004). Although there are indications of some long-term (>20 years) recovery of *R. muscosa* following stocking termination in national parks (Knapp et al. 2001; Knapp et al. 2005), I did not find any significant differences between stocked lakes and stocking-suspension lakes in densities of trout or frogs in 3 years following suspension of stocking. Additional monitoring will be necessary to reveal whether frogs respond to decreasing densities of fish and when populations begin to recover following stocking cessation. Cessation of stocking appears to be a useful long-term management option for restoring frog populations across large areas, but short-term stocking suspension does not seem to aid in frog recovery.

Acknowledgments

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