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Effects of Flow Regimes Altered by Dams on Survival, Population Declines, and Range-Wide Losses of California River-Breeding Frogs

SARAH J. KUPFERBERG,*§ WENDY J. PALEN,† AMY J. LIND,‡ STEVE BOBZIEN,**
ALESSANDRO CATENAZZI,†† JOE DRENNAN,‡‡ AND MARY E. POWER*

*Department of Integrative Biology, University of California, Berkeley, 2033 Valley Life Sciences Building, Berkeley, CA 94702, U.S.A.
†Earth to Ocean Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, BC, V5A 1S6, Canada
‡USDA Forest Service, Pacific Southwest Research Station, 1731 Research Park Drive, Davis, CA 95618, U.S.A.
**East Bay Regional Parks, 2950 Peralta Oaks Ct., P.O. Box 5381, Oakland, CA 94605, U.S.A.
††Department of Biology, Gonzaga University, 502 E. Boone Ave, Spokane, WA 99201, U.S.A.
‡‡Garcia and Associates, 2601 Mission St., Suite 600, San Francisco, CA 94110, U.S.A.

Abstract: *Widespread alteration of natural hydrologic patterns by large dams combined with peak demands for power and water delivery during summer months have resulted in frequent aseasonal flow pulses in rivers of western North America. Native species in these ecosystems have evolved with predictable annual flood-drought cycles; thus, their likelihood of persistence may decrease in response to disruption of the seasonal synchrony between stable low-flow conditions and reproduction. We evaluated whether altered flow regimes affected 2 native frogs in California and Oregon (U.S.A.) at 4 spatial and temporal extents. We examined changes in species distribution over approximately 50 years, current population density in 11 regulated and 16 unregulated rivers, temporal trends in abundance among populations occupying rivers with different hydrologic histories, and within-year patterns of survival relative to seasonal hydrology. The foothill yellow-legged frog* (Rana boylii)*, which breeds only in flowing water, is more likely to be absent downstream of large dams than in free-flowing rivers, and breeding populations are on average 5 times smaller in regulated rivers than in unregulated rivers. Time series data (range = 8 − 19 years) from 5 populations of yellow-legged frogs and 2 populations of California red-legged frogs* (R. draytonii) *across a gradient of natural to highly artificial timing and magnitude of flooding indicate that variability of flows in spring and summer is strongly correlated with high mortality of early life stages and subsequent decreases in densities of adult females. Flow management that better mimics natural flow timing is likely to promote persistence of these species and others with similar phenology.*

Keywords: amphibian declines; hydropower, natural flow regime, pulsed flows, *Rana boylii*, *Rana draytonii*

Efecto del Régimen de Flujos Alterado por Presas sobre la Supervivencia, Declinación Poblacional y Pérdidas en el Rango de Distribución de Ranas Reproductivas en Ríos de California

Resumen: *La alteración generalizada de los patrones hidrológicos debida a presas en combinación con la demanda de energía y agua durante el verano ha resultado en frecuentes pulsos de flujo atípicos en ríos de Norteamérica occidental. Las especies nativas en esos ecosistemas han evolucionado con los ciclos anuales predecibles de inundación-sequía; por lo tanto, sus probabilidades de persistencia puede decrecer en respuesta a la disrupción de la sincronía estacional entre condiciones de bajo flujo estable y la reproducción. Evaluamos si los regímenes de flujo alterados afectaron a 2 especies de ranas nativas en California y Oregon (E.U.A.) en cuatro extensiones espaciales y temporales. Examinamos la distribución de especies a lo largo de casi 50*

§email skupferberg@gmail.com
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años, la densidad poblacional actual en 11 ríos regulados y 16 no regulados, las tendencias temporales en la abundancia de poblaciones ocupando ríos con historias hidrológicas diferentes, y los patrones anuales de supervivencia en relación con la hidrología estacional. Rana boylii, que se reproduce solo en agua corriente, tiene mayor probabilidad de ausencia río debajo de presas grandes que en ríos con flujo libre, y las poblaciones reproductivas en ríos regulados son en promedio 5 veces que en ríos no regulados. Los datos de series de tiempo (rango = 8-19 años) de 5 poblaciones de R. boylii *y 2 poblaciones de* R. draytonii *a lo largo de gradientes de sincronía estacional y magnitud de inundación desde naturales hasta altamente artificales indican que la variabilidad de flujos en primavera y verano esta fuertemente con elevada mortalidad en las primeras etapas de vida y subsecuentes disminución en la densidad de hembras adultas. Es probable que el manejo de flujos que mejor se asemeje a la sincronía natural promueva la persistencia de estas especies y otras con fenología similar.*

Palabras Clave: flujos en pulsaciones, declinaciones de anfibios, energía hidroeléctrica, *Rana boylii*, *Rana draytonii*, régimen de flujo natural

Introduction

Widespread alteration of natural hydrologic patterns in rivers by dams affects a diverse array of species (Richter et al. 1997; Bunn & Arthington 2002). Some flow perturbations result from intentional management actions, such as releases and diversions outside of natural flow timing (hereafter aseasonal flows), to generate electricity and deliver water elsewhere or to augment flows via diversions from one stream segment into another. During high flows that exceed the capacities of a dam's gates or valves, there can be uncontrolled flows from reservoirs via spillways (hereafter spills). If dam operations mimic natural patterns of daily, seasonal, and annual variation in river flow, geomorphic processes, riverine species, and food webs are more likely to be sustained (Power et al. 1996; Richter et al. 2003; Poff et al. 2010). Such operations, however, often conflict with demands for energy production and water. This conflict is particularly apparent in Mediterranean climates, where runoff is highest during wet winters, but electrical and agricultural demands for water peak during dry summers (Grantham et al. 2010).

When river regulation alters the timing of historical free-flowing conditions, species that evolved with predictable (sensu Colwell 1974) annual flood-drought cycles are vulnerable to disruption of the synchrony between stable low-flow conditions and reproduction (Bunn & Arthington 2002; Lytle & Poff 2004). For example, the timing of spawning, hatching of eggs, and rearing of juveniles in anadromous Pacific salmon (*Oncorhynchus* spp.) is shaped by the seasonal cycles of runoff (Beechie et al. 2006), and ill-timed flow fluctuation can scour or dewater eggs and kill fry. Freshwater mussels (Margaritiferidae and Unionidae), a highly threatened group (Ricciardi & Rasmussen 1999), release larvae (which encyst in fish gills) in synchrony with periods of low flow. Aseasonal high flow releases can interfere with dispersal of larvae to hosts and settlement in the substrate after leaving hosts (Layzer & Madison 1995). Conversely, when natural disturbance regimes are suppressed, river hydrology often becomes more similar among regions with disparate seasonality (Poff et al. 2007), facilitating the recruitment of nonnative species (Moyle & Light 1996). Effects of unnaturally timed flows, however, have received relatively little attention in studies of the effects of river regulation (Poff & Zimmerman 2010).

The competing demands of conservation of biological diversity and human use of rivers are epitomized in California, which has double the number of hydroelectric dams (Hall 2006) and the highest total species diversity of any U.S. state (NatureServe 2010). Although regional patterns of species decline often develop from the cumulative effect of hydrologic alteration to many different rivers, most flow management decisions are made at the level of flow schedules for individual dams. In the United States, these schedules are stipulated in 30- to 50-year licenses from the Federal Energy Regulatory Commission. In California alone, approximately 50 multidam licenses were scheduled for review and renewal between 2005 and 2020 (Rehn 2009), and amphibians are being considered in the relicensing process in light of their global decline (Wake & Vredenburg 2008). However, the large number of dams and the complexity of these large watersheds can easily surpass the capacity of scientists to evaluate potential effects on a river-by-river or species-by-species basis. The situation in California's rivers exemplifies the global intensity of water resource development in which regional approaches to evaluating relations between flow management and the persistence of native riverine biota are needed to inform decision making (Poff et al. 2010).

To evaluate the regional effects of flow regime on amphibians in California, we integrated independently conducted research with local data collected in relation to the Federal Energy Regulatory Commission relicensing of hydroelectric projects. We focused on the foothill yellow-legged frog (*Rana boylii*), a California state species of special concern (Jennings & Hayes 1994), and the California red-legged frog (*Rana draytonii*), a species listed as threatened under the U.S. Endangered Species Act.

(Hereafter, we refer to these species respectively as yellow-legged frog and red-legged frog.) Yellow-legged frogs breed exclusively in flowing water and have disappeared from 54% of their range, whereas red-legged frogs use lentic and lotic habitats and are absent from 68% of historic locations (Davidson 2004). The life cycle of both species includes adult migration from tributaries and refugia to mate and oviposit on the margins of sunlit rivers during the transition between wet and dry seasons when flood probability is declining and algal food for tadpoles is beginning to bloom. Tadpoles metamorphose by late summer and juveniles move out of the river channel during autumn rains. This sequence is disrupted by releases of water from dams and spills, which can scour embryos (Lind et al. 1996) and generate velocities lethal to tadpoles (Kupferberg et al. 2011). For yellow-legged frogs, we examined survival in relation to seasonal hydrology, abundances in 11 regulated and 16 unregulated rivers, and range-wide distribution change in relation to dams. For both species, we compared temporal trends in abundance among rivers with different hydrologic histories. The seasonal synchrony between stable low flow conditions and the presence of early life stages is common to many native riverine taxa in the region and suggests that individuals in early life stages are less likely to survive if the synchrony is disrupted.

Methods

Regional Occurrence

To determine whether presence of dams is associated with changes in distribution, we mapped sites occupied by yellow-legged frogs prior to 1975 (hereafter historic sites), assessed current presence or absence, and evaluated dam-related variables (number, proximity, and size). For California we began with a database compiled from museum records and field notes on 1049 historic sites (Jennings & Hayes 1994; Davidson et al. 2002). We randomly selected 10 sites from each county in which yellow-legged frogs occurred. If a county had $\leq$10 sites, we used all its sites. We entered site locations into a geographic information system (GIS). For Oregon we identified 90 historic sites from museum and other records (Borisenko & Hayes 1999) with sufficient detail for mapping. To determine current presence or absence at California historic sites, we reviewed field accounts (Jennings & Hayes 1994; Jennings 1996), queried species experts, and conducted field surveys. Experts had information on occurrence at 53% of sites. We used field accounts (late 1980s through early1990s) and conducted summer surveys (2000–2002) to determine presence at the remaining 47% of sites. For Oregon all historic sites were surveyed 1997–1998 by Borisenko and Hayes (1999) and Borisenko (2000). The final sample size was 394 (310 California, 84 Oregon) historic sites for which we could determine occurrence on average 54 years (California) and 53 years (Oregon) after the original record.

We determined the number, proximity, and size of dams associated with each historic site from existing databases. We used ARC macro language scripts to delineate watersheds, identify dams, and calculate the distance between each dam and frog site (C. Davidson, personal communication 2011) (ArcGIS 8.3, Environmental Systems Research Institute, Redlands, California). For each California historic site, we counted the number of upstream dams, used criteria from the International Commission on Large Dams (1997) (Table 1) to categorize dam size, and calculated the ratio of total reservoir area to watershed area. For Oregon we lacked data on dam size and reservoir area, so for the combined California and Oregon data set, we restricted the analyses to presence or absence of upstream dams (Supporting Information).

We conducted chi-square contingency analyses to assess presence of dams relative to yellow-legged frog presence, 2-sample t tests with unequal variances to compare mean values of dam-related variables between historic sites where frogs are currently present or absent, and calculated Pearson product-moment correlations (r) to evaluate whether presence or absence of frogs was associated with dam variables. To reduce the likelihood of type II errors given environmental heterogeneity across an extensive area, we set alpha = 0.10.

Abundances in California

For 27 sites where yellow-legged frogs were present, we compiled results of breeding censuses we conducted with those of other academic researchers, government agencies, and utility companies (Fig. 1a & Supporting Information). Many ranid frogs lay one discrete clump of eggs (hereafter clutch) per year, and the number of clutches is commonly used as an index of population size (Loman & Andersson 2007). Clutches are readily visible on rocks to which they are attached (Fig. 1c), even after stranding (Fig. 1d) and desiccation (Supporting Information). With a general linear model (GLM), we tested whether abundances differed between regulated and unregulated rivers and whether abundances differed between coastal populations, for which peak river flow is driven by winter rainfall, and montane populations, for which peak river flow is driven by snowmelt. We report the coefficients (effect sizes) and significance of the main effects of geographic location and hydrologic status, and their interaction, on average density of clutches (ln[clutches/km]).

Temporal Trends

We evaluated 5 populations of yellow-legged frogs and 2 of red-legged frogs in watersheds (Fig. 1) spanning

Table 1. Current foothill yellow-legged frog (*Rana boylii*) presence or absence[a] at sites in California occupied prior to 1975 and characteristics of upstream dams.

Sites included in analyses and dam characteristics	*Present mean (SE)*	*Absent mean (SE)*	*Test results*[b]
All sites			
number of all dams in watershed	1.83(0.44)	3.44(1.38)	ns
number of large dams[c] in watershed	0.85(0.19)	1.36(0.38)	ns
number of very large dams[d] in the watershed	0.24(0.06)	0.50(0.14)	$t = 1.72$, $p = 0.09$; r ns
reservoir : watershed area ratio (%) (all reservoirs)	0.34(0.09)	0.32(0.08)	ns
Sites with upstream dams[e]			
distance to closest dam (km) $n_{\mathrm{present}} = 46$, $n_{\mathrm{absent}} = 39$	11.23(1.58)	9.11(1.67)	ns
distance to closest large[c] dam (km) $n_{\mathrm{present}} = 35$, $n_{\mathrm{absent}} = 37$	12.65(2.12)	9.83(1.78)	ns
distance to closest very large[d] dam (km) $n_{\mathrm{present}} = 19$, $n_{\mathrm{absent}} = 26$	19.64(5.52)	15.27(3.20)	ns
dam height (m) $n_{\mathrm{present}} = 46$, $n_{\mathrm{absent}} = 39$	40.78(5.51)	62.54(7.35)	$t = 2.37$, $p = 0.02$; $r = -0.26$, $p = 0.02$

[a] *Total n = 157 present and 153 absent.*
[b] *Two-sample t tests comparing mean values at sites where yellow-legged frogs were present and absent and Pearson product-moment correlations (r) between occupancy and dam covariates (ns, not significant). To reduce the likelihood of type II errors given the variability that exists across the area we studied, alpha = 0.10.*
[c] *Dams >15 m high; or >10 m high and > 500 m long at crest of dam; or with >1 × 10^6 m^3 storage capacity (ICOLD 1997).*
[d] *Dams >30 m high.*
[e] *Sample sizes differ because there were different numbers of dams in each size category.*

a range of hydrologic conditions (census methods and site locations detailed in Supporting Information). Each spring we searched for clutches while wading or snorkeling along river segments (hereafter reaches) that varied in sampled length according to property boundaries and dam locations. We sampled 5.2 km of the free-flowing south fork of the Eel River (1992–2010) at the University of California's Angelo Coast Range Reserve (Mendocino County); a 7.6-km reach below Cresta dam and an 8.3-km reach below Poe dam in the north fork of the Feather River (2002–2010) in Lassen National Forest (Plumas County); 2 reaches of Alameda Creek, a 1.6-km unregulated reach (Ohlone, 1997–2010) and a 1.5-km reach regulated by Calaveras Reservoir (Sunol, 2003–2010) in the East Bay Regional Park District (Alameda County), where both species occur. (Hereafter, we omit fork designations and refer to the Eel and Feather Rivers). We marked all clutches, monitored survival (i.e., hatched, stranded, scoured), and conducted biweekly censuses until all surviving clutches had hatched (Fig. 1e).

We used generalized least squares (GLS) time series models to evaluate trends in clutch density. The response variable was ln(clutches/km + 0.01) to include years when no clutches were laid. Where multiple reaches are present within a watershed, we estimated variances separately by reach (within-group heteroscedasticity) (Pinheiro & Bates 2000). We used maximum likelihood to evaluate goodness of fit for all models that included an intercept term, the variables time and reach, and a time × reach interaction. The autocorrelation structure (time-correlated errors) (Pinheiro & Bates 2000) of each time series was fit with 1-, 2-, and 3-year lags and the autocorrelation coefficients were also included as factors in the candidate model sets. We evaluated models with Akaike's information criterion for small samples sizes (AIC$_c$) (Burnham & Anderson 2002) and considered models with AIC$_c$ difference (AIC$_c$) < 1 as having the best support given the data.

Our a priori hypothesis was that variability in abundance differs on the basis of degree of flow regulation. Specifically, we hypothesized that at the unregulated Eel River, yellow-legged frog clutch density is stable (intercept only model). For Alameda Creek, we hypothesized that clutch densities upstream of Calaveras Dam are higher than downstream for yellow-legged and red-legged frogs (reach model). In the Feather River, the Cresta reach was subjected to multiple summer releases for whitewater boating from 2002 to 2005, whereas the Poe reach was not. We hypothesized that trends in yellow-legged frog clutch density diverge over time (time × reach model) in these reaches.

Hydrologic Drivers

To examine hydrologic drivers of population processes, we compiled discharge records for each watershed

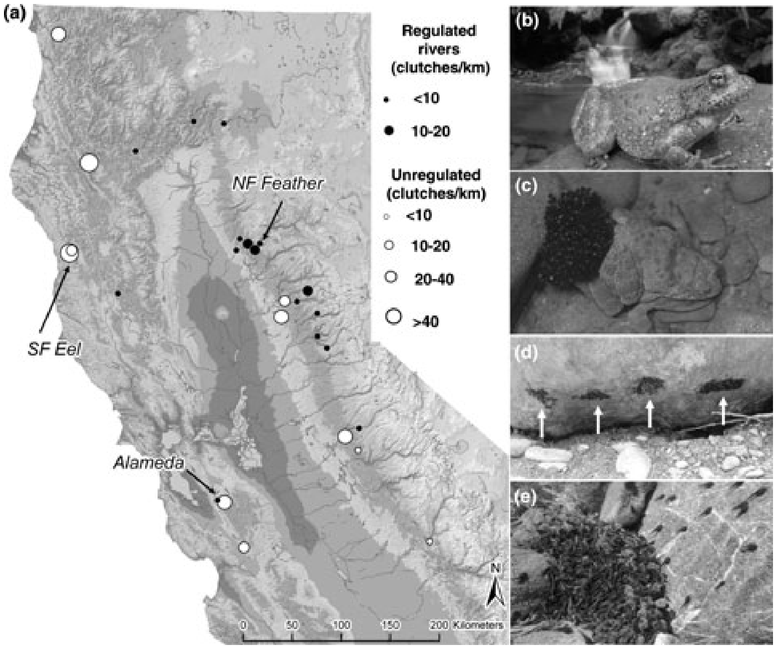

*Figure 1. Locations (a) of focal watersheds in California (Alameda Creek, north fork [NF] of the Feather River, south fork [SF] of the Eel River) and locations and average clutch densities at sites occupied by foothill yellow-legged frog (*Rana boylii*) (b) where breeding censuses have been conducted (circles) in regulated and unregulated rivers. Clutches (c) are attached to rocks, and remain visible if stranded (d) or until hatching (e).*

(Supporting Information) and tested life-stage specific hypotheses. We hypothesized that if adult frogs are susceptible to winter flooding, then there is a negative correlation between maximum winter discharge and annual change in abundance ($\lambda = N_{t+1}/N_t$, where N is number of clutches and t is year). For embryos we hypothesized that survival to hatching and the magnitude of the flow pulse during the breeding season (calculated as the ln[maximum: minimum daily mean discharge] between the day we observed the first clutches and 2 weeks after the last clutches were laid) are negatively correlated.

For the Feather River where tadpoles experienced summer pulsed flows, we hypothesized a lagged response in inferred adult density (clutches per kilometer). The lag corresponds to the time for affected cohorts of tadpoles to reach reproductive age. Growth curves fit from mark-recapture data (J.D., unpublished) indicate female yellow-legged frogs become gravid at the Feather River for the first time at age 3 years. Data from the unregulated Eel River independently suggest a 3-year lag between exposure of early life stages to scouring flows and annual decreases in census counts of clutches or benign conditions and increases in the annual census counts (Supporting Information). To compare differences in clutch density between the Cresta and Poe reaches before and after summer pulses for boating (2002–2005, Cresta only), we used before-after-control-impact analysis of variance (BACI ANOVA) (Underwood 1994). We incorporated the 3-year lag by treating 2002–2004 as before-pulsed-flow data, and 2005–2008 as after-pulsed-flow data.

Results

Regional Occurrence

For California presence of dams in the upstream watershed was associated with an absence of frogs. Compared with sites where frogs were present, there were an average of 1.9, 1.6, and 2.1 times more dams (all sizes), large dams, and very large dams, respectively, upstream of sites where frogs were absent at the time of our study, but present before 1975. The difference in the number of very large dams was statistically significant ($t = 1.72$, $p = 0.09$, df = 204) (Table 1). For sites with at least one dam upstream, the average dam height at sites where frogs were present was 22 m lower than at sites where frogs were absent at the time of our study ($t = 2.37$, $p = 0.02$, df = 73.2) (Table 1). The closest dam was farther upstream from sites where frogs were present than from sites where it was absent, but the relation was not statistically significant. Range wide (California and Oregon), the relation between presence of dams and presence of frogs at the time of our study was not significant (χ^2 contingency analysis).

Abundances in California

Among 27 sites with yellow-legged frogs (Fig. 1), mean abundance in rivers with dams was 5.5 clutches/km (SE 1.2), 5.6 times lower than in free-flowing rivers (mean of 31.1 [9.2]) (GLM of ln[clutches/km] effect size = 2.89, 95% CI 1.35–4.42, $p < 0.001$). Abundances in coastal and montane watersheds were not different (effect size = 0.85, 95% CI –0.55–2.24, $p = 0.22$), and the interaction

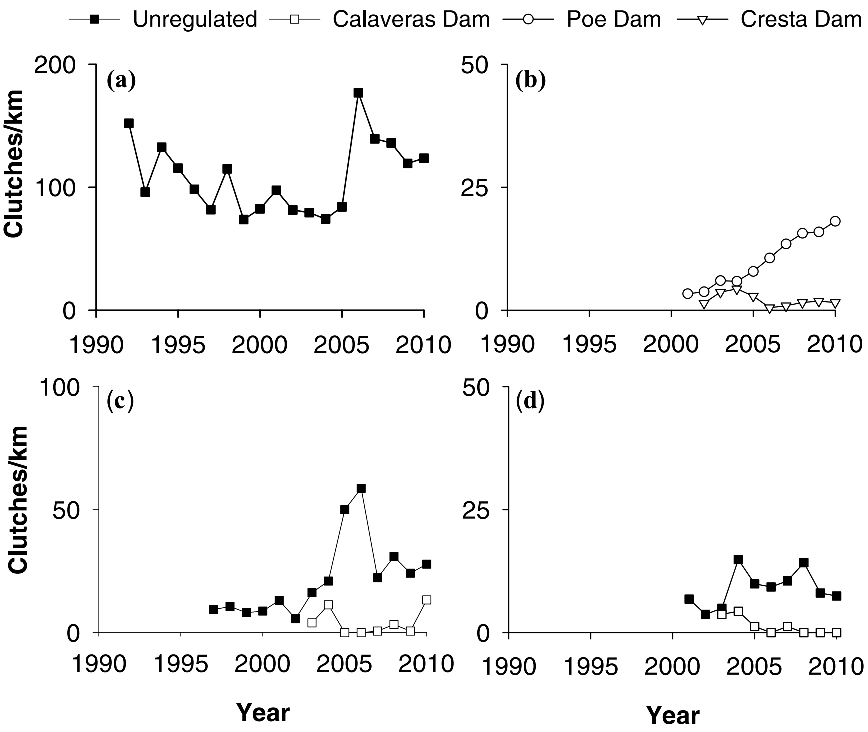

*Figure 2. Time series of clutch densities by watershed for foothill yellow-legged frogs (*Rana boylii*) in (a) south fork Eel River (5.2 km), (b) north fork Feather River (8.3 km Poe reach; 7.6 km Cresta reach), and (c) Alameda Creek (1.9 km Ohlone reach; 1.6 km Sunol reach regulated by Calaveras Dam) and for (d) California red-legged frogs (*Rana draytonii*) in the same reaches of Alameda Creek. Unregulated means no upstream dams or water diversions. The y-axis scales differ among panels.*

between region and regulation of flow was not statistically significant (effect size $= -1.63$, 95% CI $= 3.55$–0.28, $p = 0.09$).

Temporal Trends

Clutch density in the Eel River (Fig. 2a) was stable for 19 years (geometric mean $\lambda_G = 1.00$, CI 1.15–0.87, range 0.63–2.10). The most strongly supported GLS model included autocorrelation (1-year lag) and an intercept term (Table 2), but not time, which indicates there was no temporal trend.

Trends in frog abundances in the Poe and Cresta reaches of the Feather River diverged (Fig. 2b). The most strongly supported GLS model of clutch density included a time × reach interaction and 1-year autocorrelation (Table 2) and had a negative coefficient for the Cresta reach, and a positive coefficient for Poe, where there were no summer boating flows. This model estimated 5 times greater variability in annual clutch density in the Cresta reach than in the Poe reach.

From 2003 through 2010 in Alameda Creek, support was nearly equal for GLS models of yellow-legged frog clutch density that included either the intercept and 1-year autocorrelation or reach and 1-year autocorrelation (model weights 0.36 and 0.33) (Table 2). A post hoc comparison of clutch densities with the full time series (1997–2010 in Ohlone) revealed that the density of the population in the unregulated reach (Fig. 2c) was on average 5.9 times greater than in the regulated reach ($t = 3.3$, df $= 8$, $p = 0.01$). For red-legged frog, the most strongly supported model included a time × reach interaction and 1-year autocorrelation, which indicates that densities diverged over time (Fig. 2d). Variance in clutch density was 4.3 times greater for red-legged frog and 6.5 times greater for yellow-legged frog in Sunol (regulated) than in Ohlone (unregulated).

Hydrologic Drivers

At unregulated sites, peak flows occurred in winter; there were smaller, infrequent spring floods, and stable low flows throughout summer (Fig. 3a, c). Regulated sites had large-magnitude flows in late spring and summer (Fig. 3b, c): short-duration releases for recreational boating (Cresta), spills followed by rapid reductions to reserve water for future power production (Poe), and sustained releases to reduce reservoir level and thereby maintain dam seismic safety (Sunol).

Clutch survival was negatively correlated ($p < 0.05$) with the ratio of maximum: minimum discharge after oviposition commenced in all populations except that in the Poe reach of the Feather River ($p = 0.07$) ($r_{\mathrm{Eel}} =$ -0.87; $r_{\mathrm{Poe}} = -0.60$; $r_{\mathrm{Cresta}} = -0.85$; $r_{\mathrm{Ohlone}} = -0.81$; $r_{\mathrm{Sunol}} = -0.85$) (Fig. 4a). The Poe reach data included an outlier, a pulsed flow in 2005 that scoured relatively few clutches because it occurred before most were laid.

In the Eel River, Poe reach of the Feather River, and Ohlone reach of Alameda Creek, correlations between annual change in clutch density (λ) and peak winter flow

Table 2. Best supported ($\Delta AIC_c < 1$) generalized least-squares models of frog density (ln[0.01 + clutches/km]) in 3 California watersheds accounting for autocorrelation structure of 1-, 2-, and 3-year lags (AR1, AR2, AR3 respectively) and differences in variance among reaches with different hydrologic histories.[a]

Species, location (time), and model (SD ratio)[b]	K	*AIC_c*	*ΔAIC_c*	w	*Negative log likelihood*	*Phi*[c]	*Factor*	*Coefficient*	*SE*	t	p
Rana boylii											
south fork Eel River (1992–2010)											
intercept + AR1	3	6.81	0	0.66	0.39	0.40	intercept	4.67	0.09	52.4	<0.001
Alameda Creek (2003–2010)											
intercept + AR1 (1:7.4)	4	62.24	0	0.36	−25.5	0.54	intercept	3.23	0.29	11.1	<0.001
reach + AR1 (1:6.5)	5	62.44	0.2	0.33	−23.2	0.19	intercept	3.34	0.18	18.2	<0.001
							reach	−3.51	1.21	−2.9	0.01
north fork of the Feather River (2002–2010)											
time × reach + AR1 (1:5.0)	7	27.36	0	0.34	−1.08	0.14	intercept	157.40	185.6	0.85	0.410
BACI							time	−0.08	0.1	1.99	0.412
							reach	−547.30	189.3	−2.89	0.012
							time × reach	0.27	0.09	2.90	0.012
time + reach + AR1 (1:5.0)	6	27.38	0.02	0.33	−3.87	0.47	intercept	−379.20	48.9	−7.75	<0.001
							time	1.71	0.46	3.69	0.002
							reach	0.19	0.02	7.76	<0.001
Rana draytonii											
Alameda Creek (2003–2010)											
time × reach + AR1 (1:4.3)	7	58.6	0	0.51	−15.3	0.59	intercept	11.12	76.57	0.1	0.89
							time	−0.01	0.04	−0.1	0.91
							reach	2114.37	338.5	6.3	<0.001
							time × reach	−1.06	0.17	−6.3	<0.001

[a] *Abbreviations:* K, *number of fixed parameters; AIC_c, value of Akaike's information criterion for small sample sizes; ΔAIC_c, ratio of AIC_c relative to smallest AIC_c;* w, *weight of support for that model given the set considered.*

[b] *For models that allow errors to vary as a function of reach, we show the standard deviation ratio (SD ratio) of variance in clutch density comparing Oblone:Sunol reaches in Alameda Creek and Poe:Cresta reaches in the north fork of the Feather River. Full set of candidate models is in Supporting Information.*

[c] *Autocorrelation coefficient.*

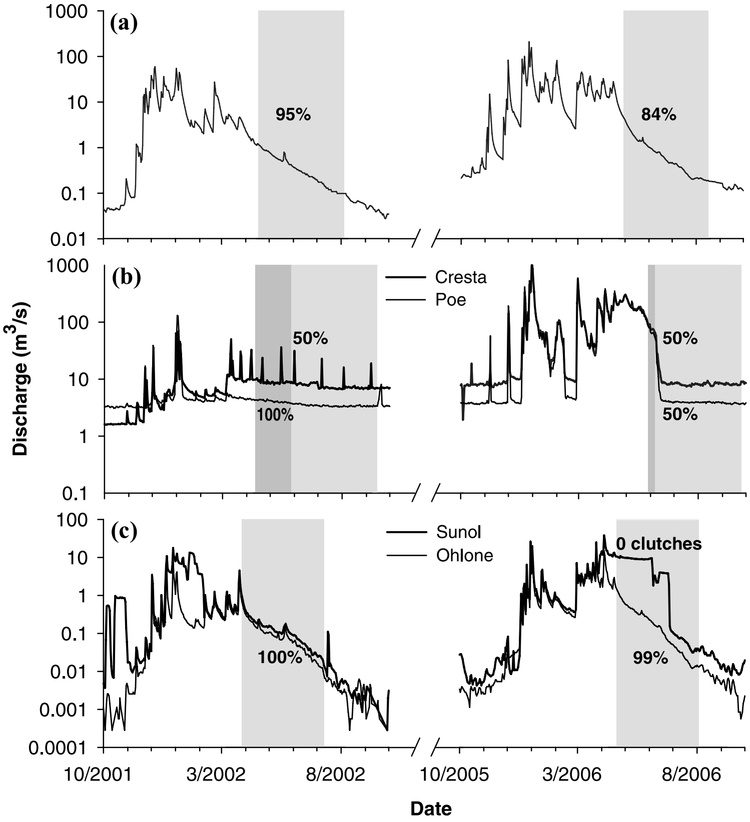

*Figure 3. Annual hydrographs from 2001 through 2002 and 2005 through 2006 for (a) south fork of the Eel River, (b) north fork of the Feather River, and (c) Alameda Creek (light gray, time of breeding and larval rearing of foothill yellow-legged frog [*Rana boylii*]; dark gray, earlier breeding in the Poe reach; percentages adjacent to hydrograph lines, survival of clutches for each year and river reach).*

were not significant (Fig. 4b). For Cresta there was a negative correlation ($r = -0.71$, $p = 0.05$), and the data relating peak winter flow with lambda were too few for analysis in Alameda Creek, Sunol reach.

For the first 3 years of summer pulsed-flow releases that affected tadpoles in the Cresta reach, trend in clutch density was similar to the Poe reach of the Feather River. After the 3-year lag to reproductive maturity, trajectories of clutch density diverged, as indicated by a significant interaction between the before versus after pulsed-flow releases and reach factors in the BACI ANOVA ($F_{1,5} = 15.4, p = 0.03$) (Supporting Information).

Discussion

Diverse lines of evidence and survey data spanning half a century indicated hydrologic alteration was associated with decreases in the distribution and abundance of yellow-legged frogs and river-breeding red-legged frogs. Yellow-legged frogs were more often absent from historic sites downstream of large dams than from sites along unregulated rivers (Table 1). Where frogs persisted, densities of reproductive adult females were on average 5.6 times smaller in regulated rivers (Fig. 1). Time series data from 7 populations spanning a gradient of natural to highly artificial timing, magnitude, and duration of flows suggested flow alteration was associated with lower abundances (Fig. 2 & Table 2) and high clutch mortality (Fig. 4a). Our results are consistent with well-documented phenomena for riverine fish: rapid water-level fluctuations can be a major source of mortality at nest sites (Cushman 1985; Grabowski & Isely 2007) and mortality events affecting early life stages can constrain populations (Strange et al. 1992).

In rivers with seasonally predictable flooding, reproduction in many taxonomic groups is timed to avoid flow fluctuations, whereas in rivers with unpredictable flooding, species often exhibit morphological and behavioral adaptations to withstand flooding (Lytle & Poff 2004). Radiotelemetry data show that the frogs we studied avoid peak flows in large channels by overwintering in tributaries (yellow-legged frogs [Bourque 2008]) or sheltering in the burrows of small mammals or in terrestrial vegetation (red-legged frogs [Tatarian 2008]). Accordingly, annual changes in clutch density, our index of adult abundance, were not closely linked to the magnitude of winter floods (Fig. 4b).

By contrast, we found that rapid changes in flow that can dislodge or strand clutches (high maximum: minimum daily discharge after spawning) were associated with low survival of clutches to hatching. Once hatched, tadpoles of yellow-legged and red-legged frogs lack the morphological features for burrowing or adhering to rocky substrates, traits seen among anurans which occur in streams where floods can happen any time of year (Altig & Johnston 1989). Field and laboratory experiments show that velocities common during pulse flows exceed the swimming ability of yellow-legged frog tadpoles and increase their predation risk (Kupferberg et al. 2011). We suggest that downstream of dams the potential for organisms to change reproductive behavior may be constrained by a lack of proximal environmental cues. Seasonal cues (day length, temperature) that trigger migration and in-stream cues (depth, velocity) that influence selection of oviposition sites (Kupferberg 1996; Grabowski & Isely 2007) are decoupled from the conditions offspring may experience weeks or months later. There may be no indication of a water release or rapid drop in water level prior to its occurrence.

The effects of disrupting the seasonality of favorable hydrologic conditions on declines in frog abundance appear to be associated with the year-to-year repetition of mortality events. At sites where abundances were stable or increasing (Eel River, Poe reach of the Feather River, Ohlone reach of Alameda Creek) embryonic mortality was lower and flow conditions were more stable than at locations with declining abundances (Cresta reach, Feather River; Sunol reach, Alameda Creek). At the Eel River, naturally occurring large-magnitude flows (discharges >20 m^3/s) during postoviposition periods were infrequent (5 of 19 years) (Supporting Information) and the effects on subsequent clutch densities were temporary. In contrast, the Cresta reach of the Feather River had 5 successive years of perturbation, summer releases for boating (2002–2005) and rapid cessation of spill during the peak snowmelt in 2006 (Fig. 3b). These conditions were unfavorable to survival of embryos and tadpoles, and the population had not recovered at the time of our study.

Our findings imply that recruitment to the adult frog population is limited by survival of embryos and tadpoles. This is not consistent with models of amphibian population dynamics, which suggest survival of postmetamorphic and adult stages are more often limiting (Biek et al. 2002; Vonesh & De la Cruz 2002). Regardless of which life stage may create a demographic bottleneck for recruitment in a given population, long-term monitoring data for amphibians indicate that large fluctuations between high and low abundance are characteristic and occasional years with high recruitment can sustain populations (Meyer et al. 1998; Daszak et al. 2005). Our results for yellow-legged and red-legged frogs highlight the potential for hydrologic events that negatively affect survival of early life stages to have a disproportionate effect on population persistence, especially if the events eliminate high-recruitment years.

At the largest spatial and temporal extents of our study, absence of yellow-legged frogs from historic sites was associated with the presence of large upstream dams (Table 1). Although it is difficult to infer flow variables

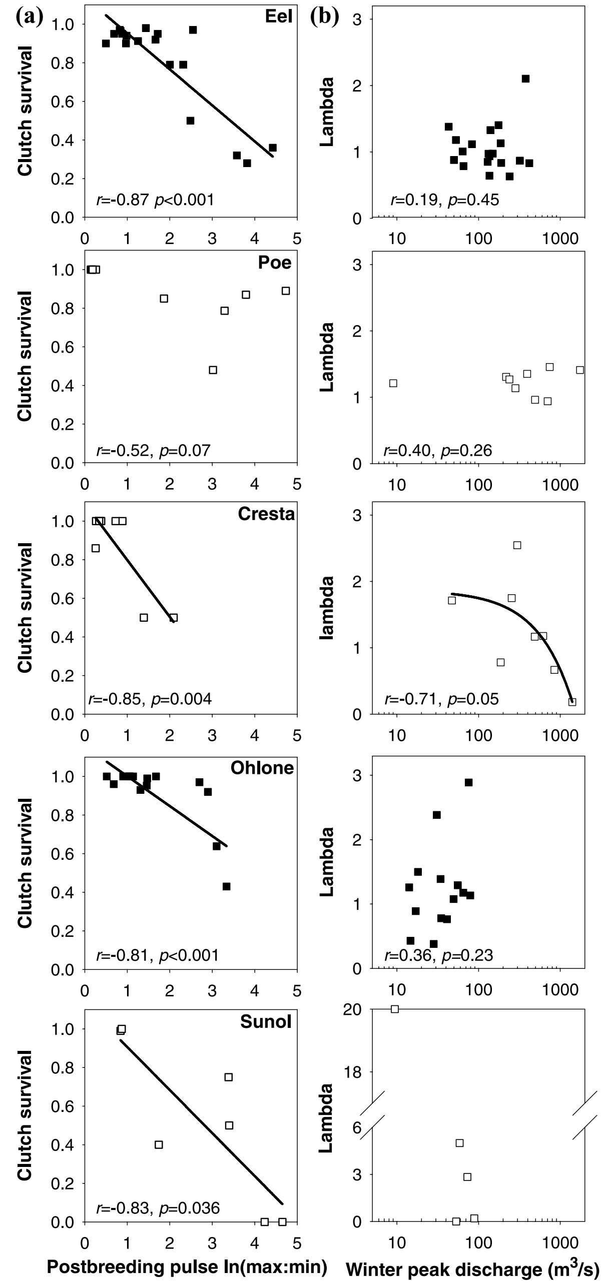

*Figure 4. Potential hydrologic drivers of abundance of foothill yellow-legged frog (*Rana boylii*) in the south fork of the Eel River, north fork of the Feather River, and Alameda Creek watersheds: (a) proportion of clutches surviving scouring and stranding as a function of the ratio of maximum to minimum daily mean discharge during embryonic development (sample sizes, number of years with survival data: $n_{Eel} = 18$; $n_{Poe} = 11$; $n_{Cresta} = 10$; $n_{Oblone} = 15$; $n_{Sunol} = 7$) and (b) annual change in abundance (lambda) inferred from clutch censuses as a function of maximum discharge ln(m^3/s) the preceding winter (open squares, regulated reaches; solid squares, unregulated; lines, significant [$p < 0.05$] Pearson product-moment correlations [r]).*

(e.g., magnitude, timing) from GIS-derived variables (e.g., dam proximity to a frog population or reservoir size), the significantly greater height of dams in watersheds where yellow-legged frogs were absent suggests a negative association between extensive hydrologic modification and population persistence. Our spatial analyses did not directly measure the geomorphic changes and nonnative predator invasions (Moyle & Light 1996) that can follow reduced peak discharge and decreased sediment supply downstream of dams. Vegetation growth in previously active channels and subsequent steepening of banks (Kondolf et al. 1996; Gordon & Meentemeyer 2006) can render areas unsuitable for frog breeding (Lind et al. 1996). We also acknowledge that dams are not randomly located, but are placed to maximize power generation and water storage. However, Lind (2005) identified no strong correlations between dam locations and agricultural and urban land use, elevation, and other factors that may be associated with changes in distribution of yellow-legged frogs. Disrupted seasonality of hydrologic conditions thus joins a list of stressors (e.g., habitat changes, disease, introduced predators) associated with amphibian declines (Wake & Vredenburg 2008).

Our results highlight that the match between seasonal hydrology and tolerances of native biota to flow fluctuation during critical life stages will determine the balance between meeting water and energy demands and protecting biodiversity. In California flow management that limits aseasonal fluctuations in discharge would likely benefit several taxa whose phenology and use of nearshore habitat is similar to that of the frogs we studied, including other amphibians (*Taricha* spp.; *Bufo* spp.), spring-spawning fish and lamprey (Brown & Ford 2002; Brumo 2006), mussels (Haley et al. 2007), and turtles (Bury & Germano 2008). These long-lived taxa have early life stages that are susceptible to high flows, and their delayed onset of sexual maturity may constrain their ability to offset losses of early life stages (Congdon et al. 1993). We focused on frogs subjected to Mediterranean seasonality of water flow. However, a wider array of species may be susceptible to disruption of the synchrony among reproduction, benign physical conditions, and abundant food because predictable patterns of seasonality have shaped the timing of life-history events in many marine, freshwater, and terrestrial taxa (Dudgeon 2000; Visser & Both 2005; Sydeman & Bograd 2009). Our results suggest that alteration of the timing of stable conditions can have disproportionate effects on early life stages and result in declines of suites of species with similar reproductive timing.

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Supporting Information

Census, GIS, and BACI analyses (Appendix S1), site characteristics (Appendix S2), and Eel River analyses (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of material) should be directed to the corresponding author.

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