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Factors that Influence the Timing of Calling and Oviposition of a Lotic Frog in Northwestern California

Clara A. Wheeler,[1] Amy J. Lind,[2] Hartwell H. Welsh Jr., and Adam K. Cummings

USDA Forest Service, Pacific Southwest Research Station, Redwood Science Lab, Arcata, California USA 95521

Abstract.—**Species that breed in stream environments with unpredictable interannual variability in hydrological regimes may exhibit plasticity in the timing of their breeding activities. Breeding phenology should coincide with conditions and habitats that maximize a species' reproductive success. For the lotic-breeding frog *Rana boylii*, the timing of breeding activities of a population can vary by more than a month among years. To examine the influence of abiotic factors on the variation in the timing of onset and patterns (i.e., peaks and pauses) in breeding activity of *R. boylii*, we sampled seven geographically separated sites that covered an extensive portion of the species' range in northwestern California for two breeding seasons. We collected daily environmental and male vocalization data and conducted weekly egg mass surveys at breeding sites. Here, we found the timing of calling activity and oviposition varied markedly among geographically separated sites and between years. Water depth and water temperature influenced calling phenology, whereas water depth and both temperatures (water and air) were significant factors in the timing of oviposition. In general, breeding activity did not commence until water temperatures reached 10°C. Calling and oviposition occurred later at deeper sites with colder, spring water temperatures. Models that predict the timing of breeding activities can improve survey and monitoring efforts and can assist managers of regulated streams in developing flow assessments that are compatible with species' breeding requirements. This information may be particularly useful in developing individual based models to assess overall reproductive success.**

Stream organisms are adapted to natural variations in hydraulic conditions, such as water depth and water velocity. They exhibit plasticity in their breeding phenology, the timing of reproductive activities, as a behavioral response to seasonal and annual variation in stream conditions. Unseasonal or extreme changes in streamflow or thermal regimes resulting from stream regulation may affect the behavior of stream breeding organisms, which may influence reproductive success (e.g., Lind et al., 1996). Furthermore, climate change may alter streamflows even more than dams and diversions and may impact populations in regulated and unregulated streams (Döll and Zhang, 2010).

Climate-related factors such as rainfall and water temperature influence the breeding activity of many anuran species, but determinants of the timing of breeding activities depend on the type of habitat used for reproduction (i.e., lake, pond, stream, or terrestrial; and perennial, ephemeral, or intermittent). The breeding phenology of anurans is strongly influenced by abiotic factors, but the influence of various factors on anuran breeding is species specific (Saenz et al., 2006). Most of the literature on anuran reproductive phenology focuses on lentic-breeding species where rainfall and temperature often trigger breeding activities. As with lentic-breeding species, temperature likely plays a role in the timing of breeding activities of lotic species, but streamflow may also be a factor (Fukuyama and Kusano, 1992). Breeding activity of stream-breeding species often occurs during respective dry seasons because streamflows during the rainy season can flood suitable calling, oviposition, and rearing habitats (Fukuyama and Kusano, 1992; Kam et al., 1998; Hsu et al., 2006).

The Foothill Yellow-Legged Frog (*Rana boylii*) is a stream-dwelling species in northern California. The flow and thermal regimes of many California rivers and streams are managed through the operation of dams and diversions, which have been identified as the primary risk to the persistence of *R. boylii* (Lind, 2005; Hayes et al., 2016). The timing of oviposition of stream-breeding *R. boylii* is important to egg mass survival (Lind et al., 1996; Railsback et al., 2016). These frogs attach their eggs to rocky substrates along stream margins in late spring and tadpoles metamorphose in late summer (Fuller and Lind, 1992; Lind et al., 1992; Wheeler et al., 2003). If frogs oviposit too soon, their egg masses are at risk of scouring or stranding (Lind et al., 1992; Kupferberg, 1996); however, late breeding activity can lead to future consequences such as late metamorphosis and smaller size or lower body condition at metamorphosis (Wheeler et al., 2015; Railsback et al., 2016). Kupferberg (1996) found evidence that the initiation of egg laying was influenced by air and water temperature; daily mean temperatures were significantly warmer one week after the first egg mass was observed compared to temperatures one week preceding egg mass detection. Within the Trinity River watershed of northern California, populations bred earlier on streams with warmer average water temperatures (Wheeler et al., 2015).

We studied calling phenology along streams across northwestern California to determine whether males and females respond to the same or different cues and to examine whether there is a relationship between when males start calling and when mating and oviposition occur (e.g., is there a predictable time lag between the behaviors?). This work expands on earlier studies that examined the effects of various environmental factors on the timing of *R. boylii* oviposition within populations and among populations within the same watershed (Kupferberg, 1996; Wheeler and Welsh, 2008; Wheeler et al., 2015). Male calling and female oviposition behaviors are clearly linked, but the environmental cues that regulate the timing of reproduction may be different for male and female organisms (Ball and Ketterson, 2008). We examined associations between dates of onset of breeding activities and geographic and environmental variables, and we analyzed the relationships between patterns in calling and oviposition activities and environmental factors.

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[1] Corresponding Author. Present address: USDA Forest Service, National Technology and Development Program, Missoula, Montana USA 59808; E-mail: cawheeler@fs.fed.us

[2] Present address: USDA Forest Service, Tahoe and Plumas National Forests, Nevada City, California USA 95959

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TABLE 1. Summary of study stream information for breeding sites sampled in northwestern California. The area variable is the size of the watershed upstream of the sampling location. We assigned snow influence categories based on the geographic location of the site, hydrographs, extent of the watershed area at higher elevations, and personal communication with a local expert (L. Reid, retired geologist, pers. comm.).

Stream/river	County	Latitude	Longitude	Elevation (m)	Snow influence	Area (km^2)	Regulated?
Hurdygurdy (HG)	Del Norte	41°41′24.8″N	123°53′44.5″W	171	Some	77	No
Red Cap (RC)	Humboldt	41°15′8.1″N	123°34′34.7″W	91	Some	163	No
Mainstem Trinity (MSTR)	Trinity	40°40′25.8″N	123°01′27.1″W	460	Much	2,523	Yes
South Fork Trinity (SFTR)	Humboldt/Trinity	40°51′42.2″N	123°34′34.7″W	168	Some	2,458	No
Mattole (MAT)	Humboldt	40°06′54.4″N	123°59′41.9″W	200	Trace	127	No
South Fork Eel (SFEEL)	Mendocino	39°44′10.3″N	123°38′42.6″W	411	Some	154	Yes
Pepperwood Ranch Trib (PW)	Sonoma	38°34′4.5″N	122°41′34.8″W	330	Trace	<1	No

We collected these data over two decades ago, not long after the Intergovernmental Panel on Climate Change first summarized climate change research (IPCC, 1990). These data represent some of the earliest comprehensive records of *R. boylii* breeding activity and corresponding environmental data and are valuable baseline data. Assessing the relationships between the timing of breeding activities and climate factors may be useful in predicting how this species might respond to climate change and in developing species persistence models and conservation strategies for this sensitive species in a changing climate. Furthermore, understanding how environmental variables affect breeding activities may be important in mitigating climate change impacts.

MATERIALS AND METHODS

Study Sites and Geographic Data.—We monitored breeding sites along six streams with known Foothill Yellow-Legged Frog populations from April through June of 1994 (Hurdygurdy Creek, hereafter HG; Red Cap Creek, RC; South Fork Trinity River, SFTR; mainstem Trinity River, MSTR; Mattole River, MAT; South Fork Eel River, SFEEL). In 1995, we added a site (a tributary of Mark West Creek at Pepperwood Ranch, PW) and monitored from March through early July. We selected streams along a north to south latitudinal gradient from 41°41′ to 38°34′ in northwestern California (Fig. 1). Study streams also varied in longitude, elevation, and hydrological influence; some sites were coastal, whereas others more inland and streams occurred in watersheds that were rain fed, snow fed, or received input from both types of precipitation (Table 1). We assigned snow influence categories (much, some, trace) based on the geographic location of the site, hydrographs, extent of the watershed area at higher elevations, and personal communication with a local expert (L. Reid, retired geologist, pers. comm.). We marked the locations of breeding sites on national forest topographic maps and later located each site using GIS software to obtain latitude and longitude coordinates and elevation data.

Environmental and Calling Data.—We modified existing designs for automated data logging and sound recording equipment (Eads, 1991; Peterson and Dorcas, 1992, 1994). At each location, we installed a data logger in a steel strong box and cable locked the box to a nearby tree or rock to limit vandalism. We programmed each data logger to measure stream water level, air temperature, and water temperature every 15 min. We installed two pressure transducers at each location to measure water level. We placed one pressure transducer within the breeding area and another in stable pool habitat near the breeding site to establish a permanent benchmark (usually a bedrock outcrop). We used pressure transducer data from benchmark sites to check the probe's accuracy and to standardize water depth data from year to year. We secured an air temperature probe to the north side of a riparian tree in the shade, and we attached a water temperature probe to a stake and placed it in or near the main flow of the stream. We positioned underwater microphones (hydrophones) in calm water to reduce background water noise with microphones located as close to the breeding site as possible to facilitate clear recordings. We set data loggers to turn on an analog tape player every 15 min from 0430 to 0730 h and from 1830 to 2130 h each day that recorded 35 sec of sound during each recording interval. We selected these recording times because males of this species are most frequently heard calling at dusk and dawn (P. Northen, pers. comm.). A voice time stamp was automatically turned on and off at the beginning of each 35-sec sampling interval. We changed audio tapes once per week. We analyzed audio tapes in the laboratory by counting the total number of calls (regardless of vocalization type) each day at each site. The function of the different vocalization types of this species has not yet been determined; however, based on personal observations of the behavior of these frogs (Wheeler and Welsh, 2008), we feel secure with the assumption that calls we recorded at breeding sites during the breeding period (and later counted) had a role in breeding behavior (e.g., long-range advertisement, short-range advertisement, and maintaining male spacing).We divided the number of daily calls by the number of recording intervals for that day.

Egg Mass Surveys.—We conducted weekly surveys for egg masses by slowly walking the stream shoreline at each breeding site. We counted the number of new egg masses and mapped and marked individual egg masses by painting small cobbles and placing them next to egg masses.

Relationship between the Onset of Calling and Oviposition.—To compare the relationship between the onset of calling and the onset of oviposition, we ran a linear regression comparing Julian day onset dates of the two behaviors, based on the date when 5% of the total activity for the year at that site was complete. The first detected call of the season can occur nearly a month before most of the calling, and we found this definition reduced the influence of early outliers and put the onset date more in line with the onset of the majority of the detected calling and oviposition. Using this threshold means the onset dates more accurately reflect breeding activities and are not biased by individual animals arriving before population-level breeding behaviors commenced. We recognize site-level variation in onset might be important to the overall pattern, but with only two years of data we were unable to control for site-level effects.

Analysis of Onset of Calling and Oviposition.—To test the importance of environmental conditions on the onset of reproductive behaviors we ran a series of linear models with the Julian onset date at each site-by-year combination as the response and environmental variables summarized to the site-by-

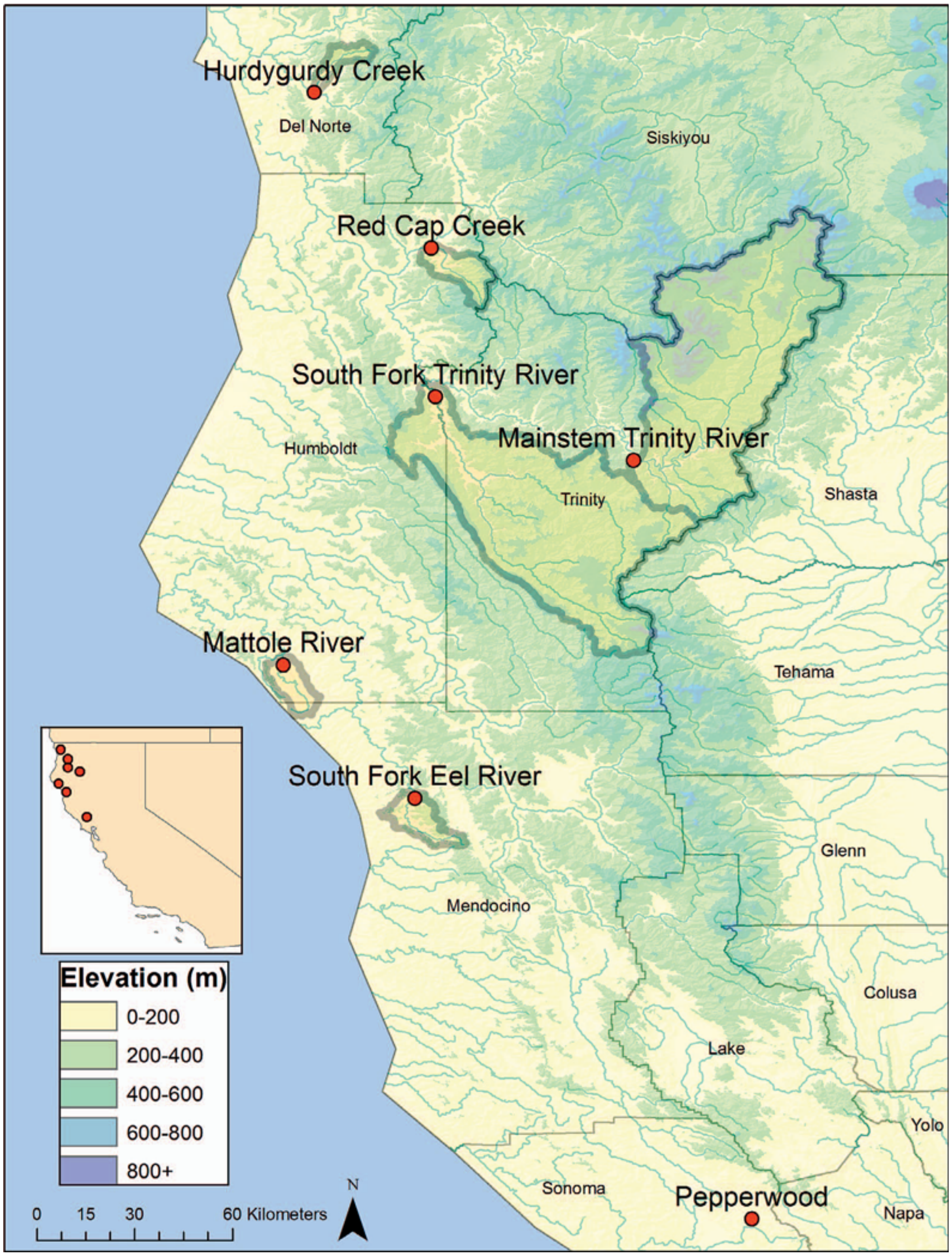

FIG. 1. Locations of streams sampled for *Rana boylii* calling and oviposition activities in northwestern California.

year level as predictors. We again defined the date of onset of calling and oviposition for each site as the first Julian day when 5% of the total activity for the year at that site was complete. We quantified the effects of geographic location (latitude, longitude, and elevation) and local environmental variables on calling and oviposition. Environmental variables included: 1) relative water depth as the difference between daily mean water depths and site-specific mean water depths measured at approximate summer low flow; and 2) average daily mean relative water depths, air temperatures, and water temperatures from 23 April to 23 May to generalize the conditions during the breeding season. We used general linear models (Program SAS, PROC-GLMSELECT) and the best model was determined based on the lowest corrected AIC (AICc), a modified version of Akaike's Information Criterion used for small sample sizes.

Analysis of Calling Activity Patterns.—To examine the relationship between environmental variables and the daily number of individual calls we detected, we used generalized linear mixed models (GLMM) with a negative binomial error distribution, log link function, and site name and year as crossed random effects intercepts (resulting in two random intercept levels for year and six for sites). The number of usable vocalization recordings was included as an offset variable to control for uneven effort within a day attributable to equipment issues. Fixed effect parameters included daily mean water depth, daily mean air temperature, and daily mean water temperature. We built a candidate model set to include permutations of the three environmental variables

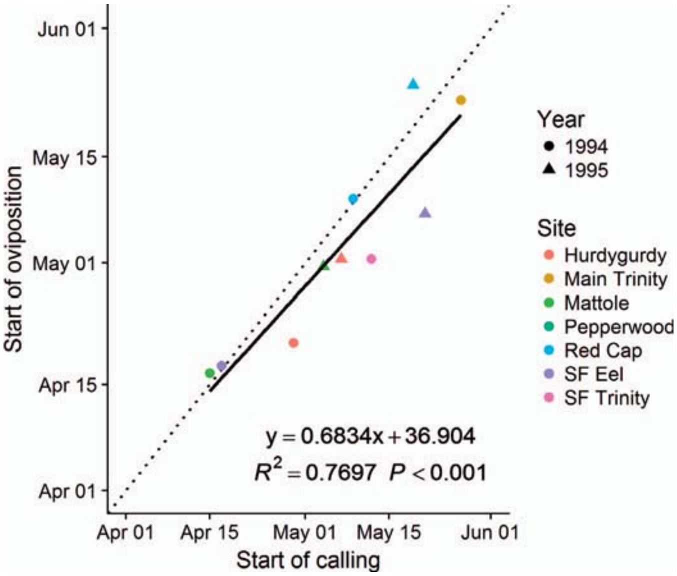

FIG. 2. Relationship between *Rana boylii* calling onset dates and oviposition onset dates for populations sampled in northwestern California. The x- and y-axes are labeled with calendar date to simplify interpretation, but the regression equation shown is based on the Julian day of onset. The dashed line shows the 1 to 1 correspondence date for oviposition and calling initiation.

in linear or linear + quadratic form (15 models). We centered and scaled all continuous parameters. We omitted three sites for 1995 (MSTR, SFTR, and RC) that had no or only a few call detections because of equipment failure and issues related to high water. This resulted in structural zeros that did not describe the true condition.

Data were analyzed in R-statistical package (R Core Development Team, 2013), and AICc was used to rank models in the multimodel inference package "MuMIn" (Bartoń, 2013). We calculated model fit parameters for the top-ranked model following Nakagawa and Schielzeth (2013) that considered the contributions of the fixed terms only, or marginal R^2 (R^2_m) and the contributions by both the fixed and random terms, or conditional R^2 (R^2_c). The difference between R^2_c and R^2_m indicates the amount of variability explained by the random effects (Nakagawa and Schielzeth, 2013).

Analysis of Oviposition Activity Patterns.—For the oviposition activity analysis, we ran a similar GLMM, with a zero-inflated Poisson distribution and log link function to model the number of egg masses detected each week. Fixed effect parameters included mean weekly maximum temperatures (MWMT) for air and water temperature variables, including quadratic forms. All sites were included in the analysis. We included a variable that quantified weekly calling activity to assess the importance of calling on oviposition activity. The analysis resulted in 16 candidate models that we ranked using AICc.

RESULTS

Onset of Calling.—Neither onset of calling nor oviposition were synchronous among sites or between years (Appendix 1). Calling onset and oviposition onset dates were related ($R^2 = 0.77$, $P < 0.001$; Fig. 2). The onset of calling did not occur at air or water temperatures below 10°C and calling generally started later at deeper water depths and cooler water temperatures: 181.84 + (0.72 × mean water depth) − (6.61 × mean water temp); $F_{2,7} = 21.48$, $P < 0.0001$, Adjusted $R^2 = 0.82$, AICc = 63.63. Averaging across sites, the onset of calling occurred 4 days later in 1995 than in 1994 (Fig. 3a,b; Appendix 1).

Onset of Oviposition.—The onset of oviposition generally did not occur at air or water temperatures below 10°C (except at HG in both years and PW in 1995; Table 2). The onset of oviposition followed the same pattern as calling, occurring later at deeper water depths and cooler temperatures: 171.21 + (0.47 × mean water depth) − (5.39 × mean water temp); $F_{2,7} = 10.09$, $P < 0.01$, Adjusted $R^2 = 0.67$, AICc = 64.37. On average, oviposition started 5 days later in 1995 than in 1994.

Calling Activity Patterns.—In general, few males called at the beginning and end of the breeding season, and calling activity peaked one or more times during the breeding season (Appendix 1). The predicted peak in calling activity occurred at water depths

TABLE 2. Water stage and temperature summary table for sites sampled in northwestern California. Dots (.) indicate missing data. HG–Hurdygurdy Creek; RC–Red Cap Creek; MSTR–Mainstem Trinity River; SFTR–South Fork Trinity River; MAT–Mattole River; SFEEL–South Fork Eel River.

	Calling onset day			Oviposition onset day			23 April to 23 May average		
	Air temp (°C)	Water temp (°C)	Depth (cm)	Air temp (°C)	Water temp (°C)	Depth (cm)	Air temp (°C)	Water temp (°C)	Depth (cm)
1994									
HG	11.79	10.61	7.85	6.66	9.63	4.46	11.40	11.14	8.15
RC	16.45	12.67	11.97	16.45	12.67	11.97	.	.	.
MSTR	16.49	15.22	4.84	13.79	10.60	5.75	13.08	10.42	61.54
SFTR	17.47	17.70	48.56	14.93	13.67	56.29	14.98	14.81	53.15
MAT	13.07	12.21	10.22	14.43	12.77	9.93	12.04	12.74	15.12
SFEEL	11.71	13.00	3.39	11.71	13.00	3.39	10.92	12.08	12.57
Mean	14.50	13.57	14.47	12.99	12.06	15.30	12.48	12.24	30.11
SD	2.60	2.51	17.00	3.47	1.57	20.35	1.61	1.69	25.17
1995									
HG	11.03	10.20	17.83	10.54	9.28	19.83	11.67	10.53	15.89
RC	15.23	11.21	16.43	17.07	12.09	15.53	13.34	10.24	20.13
MSTR	.	.	.	.	.	.	.	.	.
SFTR	.	.	.	20.79	16.72	37.34	.	.	.
MAT	10.04	10.79	36.04	11.72	11.17	30.99	11.69	11.64	26.86
SFEEL	12.89	13.10	22.82	12.89	10.33	43.56	10.42	11.06	36.02
PW	12.74	11.82	5.97	8.85	11.51	1.98	12.73	13.60	3.89
Mean	12.39	11.42	19.82	13.64	11.85	24.87	11.97	11.42	20.56
SD	1.99	1.11	10.95	4.47	2.58	15.36	1.12	1.33	12.02

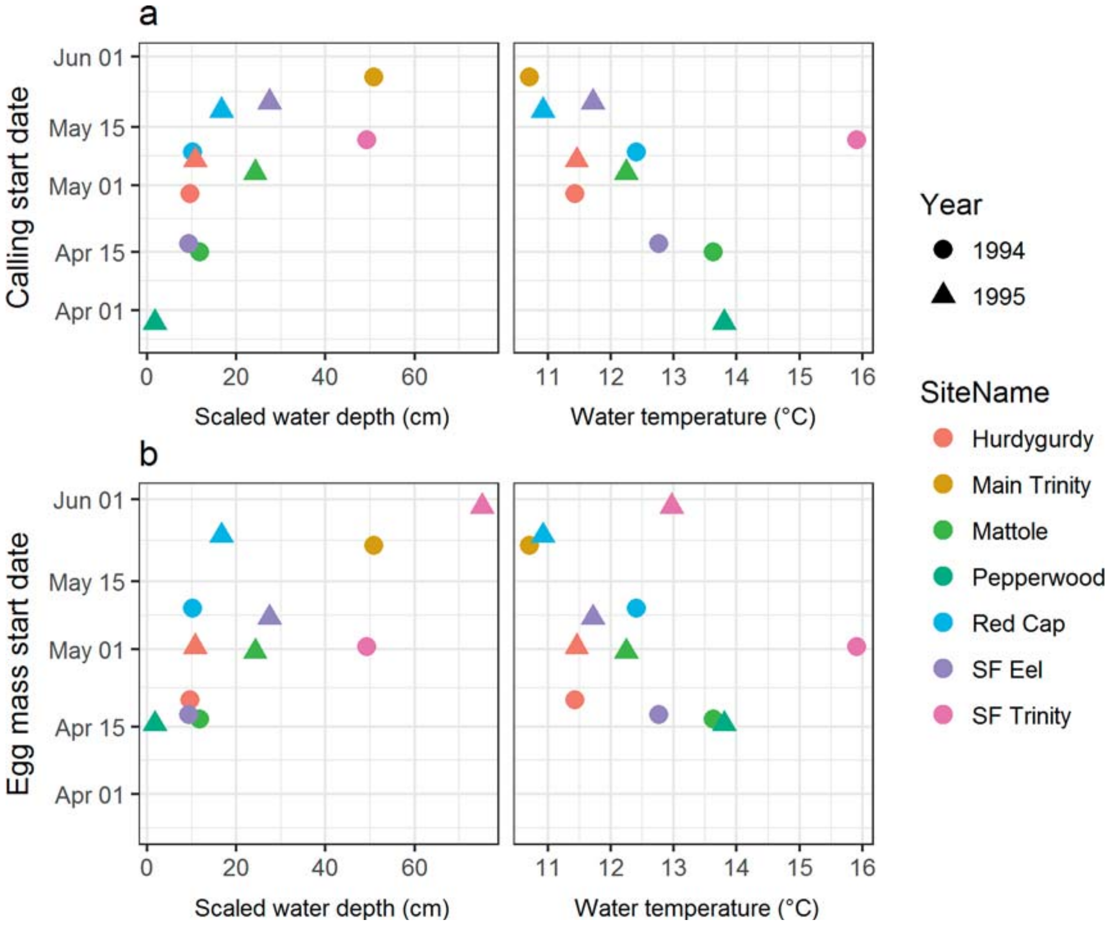

FIG. 3. Relationship between the A) initiation day of calling and scaled water depth (left) and water temperature (right); and B) initiation day of egg mass detection and scaled water depth (left) and water temperature (right). Water temperature and water depth represent the mean value from 23 April to 23 May. Colors indicate individual sites and shapes indicate survey year (1994, circle; 1995, triangle).

of ~30 cm and water temperatures of ~14°C (Akaike weight w_i = 0.76; Table 3; Fig. 4a). All other models had > 2 ΔAICc; therefore, we only interpreted the top model (Table 4). Fixed effect-terms explained 52% (i.e., $R^2_m = 0.52$), and fixed and random effects explained 89% (i.e., $R^2_c = 0.89$) of variance in calling activity, suggesting site and year have a strong influence in the overall variability in calling patterns.

Oviposition Activity Patterns.—We detected few egg masses at the beginning and end of the breeding season. The top and second ranked models for oviposition activity both included water depth, air temperature, and amount of weekly calling (w_i = 0.41 and 0.29, respectively; Table 3). Other models had >2 ΔAICc; thus, we interpreted only the top two models (Table 5). The primary difference between the two models was that the top model included quadratic terms for both water depth and air temperature. The top model predicts peak in oviposition activity occurring at water depths of ~20 cm and air temperatures of ~11°C (Fig. 4b). Fixed-effect terms explained 86% (i.e., $R^2_m = 0.86$), and fixed and random effects explained 96% (i.e., $R^2_c = 0.96$) of variance in oviposition activity, indicating variability across sites and years.

DISCUSSION

Environmental Factors.—Our results demonstrate that *R. boylii* breeding activities are influenced by water levels. The effect of the relative water depth on activities was likely the frogs' response to the temporal availability of breeding habitat (calling substrates and suitable oviposition sites). These frogs begin calling when water levels and water velocities recede following winter–spring rain and snowmelt runoff events, with reduced stream depths coincident with the availability of above water calling sites along stream edge habitats. Males of this species frequently call from emergent rocks within the stream and appear to defend calling sites within breeding areas to attract females (C. Wheeler, pers. obs.). Kupferberg (1996) found that emergent rocks were a common feature at *R. boylii* breeding sites but not at nonbreeding sites during the breeding season. In a study of another stream-breeding frog, *Buergeria buergeri*, Fukuyama and Kusano (1992) found a strong negative correlation between the amount of rainfall and the number of males that attended breeding sites, and they suggested that this could be the consequence of inundated stones used as calling substrates. For *R. boylii*, spring rainfall that maintains elevated water levels may delay the onset of calling and rain events that occur after calling has commenced may result in increased water levels or ambient noise that deter calling activity (Sun and Narins, 2005). We observed reduced calling during peaks in water depths that corresponded with rain events (Appendix 1 and Thornton et al., 2017).

In general, we detected most of the egg masses in shallow water, and the range of relative water depths was in close agreement with data from other studies (Bondi et al., 2013; Railsback et al., 2016). Frogs select microhabitats such as edge

TABLE 3. Top-ranked generalized linear mixed-effects model (GLMM) results for the effects of environmental variables on calling activity and oviposition activity of *Rana boylii*. We included quadratic versions of the water depth, water temperature and air temperature variables. Asterisks indicate level of significance: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Factor	Estimate	SE	z	P
Daily number of calls				
Intercept	0.286	0.7471	−0.38	0.701
Water depth	−0.6533	0.2845	−2.3	0.022 *
$(\text{Water depth})^2$	−0.6103	0.2056	−2.97	0.003 **
Water temp	0.5238	0.1656	3.16	0.002 **
$(\text{Water temp})^2$	−0.498	0.0828	−6.01	<0.001 ***
Weekly number of egg masses				
Intercept	1.394	0.404	3.45	<0.001 ***
Water depth	−0.408	0.244	−1.67	0.095
$(\text{Water depth})^2$	−0.583	0.277	−2.11	0.035 *
Mean weekly max air temp	−0.645	0.122	−5.31	<0.001 ***
$(\text{Mean weekly max air temp})^2$	−0.049	0.084	−0.58	0.561

water that provide stable water depths, and low water velocities, which warm up rapidly, are often dominated by cobble or boulder substrates and used for egg mass attachment and calling (Kupferberg, 1996; Wheeler and Welsh, 2008; Bondi et al., 2013; Lind et al., 2016). Frogs generally oviposit in areas where the water is deep enough to avoid stranding (desiccation) during receding spring flows and velocities at these depths are low enough to avoid scouring (Kupferberg 1996). Wide and shallow sections of streams provide higher buffering capacity (i.e., stable depths and velocities) against the risk of scouring (Yarnell et al., 2012). Egg masses are also at risk of scouring if females deposit them before or during natural storm events or artificial water releases from dams in managed systems that result in increased water velocities, and high flows may even impede breeding activities altogether in some years (this study; Kupferberg, 1996; Lind et al., 1996; Railsback et al., 2016).

Earlier studies have shown that streamflow or variables associated with flow regime strongly influence the timing of oviposition of *R. boylii* (Kupferberg, 1996; Wheeler and Welsh, 2008; Wheeler et al., 2015). Kupferberg (1996) found that *R. boylii* oviposition was timed to avoid fluctuations in water stage and stream velocity, and frogs bred earlier in low base-flow discharge years. Wheeler and Welsh (2008) similarly found that annual variation in the timing of oviposition was associated with mean streamflow during the breeding season. Water depth measurements can be used as a proxy for stream discharge, but the relationship between water depth and discharge is not linear because of the irregular shape of stream channels. We did not collect cross-sectional area or water velocity data needed to produce elevation-discharge rating curves (Kupferberg, 1996). In shallow breeding habitats, however, decreasing streamflows result in dropping water depths, and both factors appear to be conditions necessary for successful oviposition and subsequent egg mass and tadpole survival (Railsback et al., 2016).

Of the variables we examined, water temperature had the greatest effect on the onset of *R. boylii* calling and oviposition. Our results support previous studies suggesting temperature as a primary factor in the onset of oviposition of this species (Kupferberg, 1996; Catenazzi and Kupferberg, 2013; Wheeler et al., 2015). Here, we observed earlier oviposition at warmer water sites. Water temperature (especially between 13 and 15°C) also influenced the number of *R. boylii* calls we detected. The underwater calling behavior of this species and the effects of temperature on acoustics and calling energetics (Gerhardt and Huber, 2002; Wells, 2010) may explain the influence of water temperature on *R. boylii* calling activity. Similarly, Kusano and Fukuyama (1989) found the number of pairs of a stream-breeding Japanese ranid (*Rana sakuraii)* was correlated with water temperature, and annual differences in timing of breeding activity was explained by variability in water temperatures; breeding occurred later in years that remained colder longer.

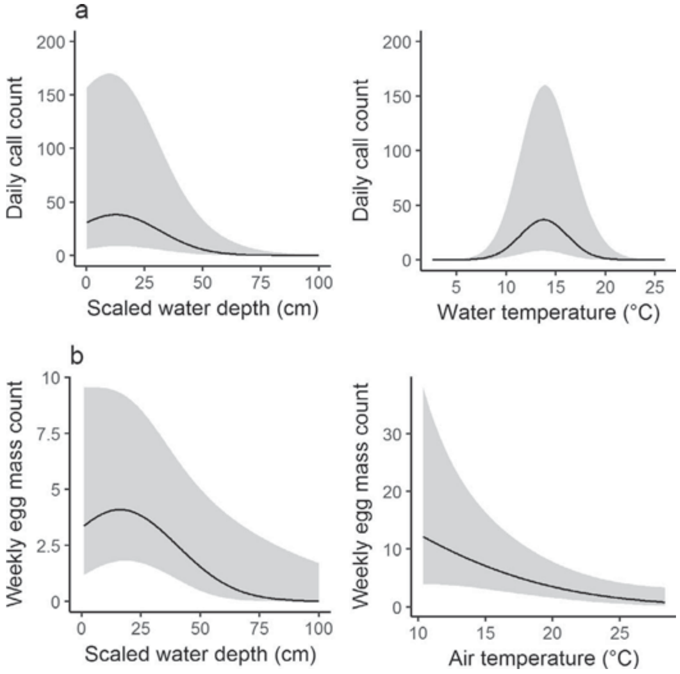

FIG. 4. Relationship between the a) predicted number of calls and scaled water depth (left) and water temperature (right); and b) predicted number of egg masses and scaled water temperature (left) and water depth (right). Predictions based on top GLMMs.

In general, temperature is the most common predictor of anuran reproductive activities (Oseen and Wassersug, 2002). Temperature has a profound effect on many aspects of anuran physiology and behavior (Hutchison and Dupré, 1992; Rome et al., 1992). Temperature can affect anuran egg and tadpole development and growth rates (Hutchison and Dupré, 1992) and temperatures experienced by embryos can have later effects on tadpole physiology (Seebacher and Grigaltchik, 2014). Species-specific lower thresholds for breeding of ranid frogs ranged 8–15°C for lower air temperatures and ranged 8–12°C for lower water temperatures (Oseen and Wassersug, 2002). The lower water temperature threshold for onset of calling and oviposition for *R. boylii* appears to be when temperatures warm to ~10°C (this study and Hayes et al., 2016).

Although water depth and water temperature influenced both the onset of calling and onset of oviposition, we could not reliably determine the relationship between when males started calling and when mating and oviposition occurred. In a six-year study of the mating strategy and breeding activity of a *R. boylii* population (the same breeding site on Hurdygurdy Creek sampled in this study), Wheeler and Welsh (2008) observed males arriving and calling before the asynchronous arrival of females and subsequent mating and oviposition. We suspect that calling activity generally occurs before mating and oviposition. In this study, however, the onset of calling and oviposition were related, but a simple regression of the onset of

TABLE 4. The generalized linear mixed model set used to examine relationship of environmental variables to number of daily calling events detected (response variable). Site and year were included as random factors. df is the number of model degrees of freedom, logLik is the likelihood of the model, AICc is the corrected Akaike's information criterion, Δ_i is the difference in AICc between the top model and model *i*, ω_i is the Akaike weight for model *i* given the model set. † Int indicates the intercept; WT, daily mean water temperature; AT, daily mean air temperature. All models also included an offset parameter to control for the number of intervals recorded each day.

Model	Model structure †	df	logLik	AICc	Δ_i	ω_i
2	Int + Depth + Depth^2 +WT + WT^2	8	−1,541.5	3,099.4	0.00	0.67
5	Int + Depth + Depth^2 +WT + WT^2 +AT + AT^2	10	−1,540.1	3,100.8	1.41	0.33
3	Int + Depth + Depth^2 +AT + AT+	8	−1,549.7	3,115.8	16.48	0.00
10	Int + Depth + AT	6	−1,555.8	3,123.8	24.41	0.00
12	Int + Depth +WT + AT	7	−1,555.1	3,124.5	25.18	0.00
13	Int + Depth	5	−1,557.6	3,125.4	26.03	0.00
6	Int + Depth + Depth^2	6	−1,556.9	3,126.0	26.65	0.00
9	Int + Depth +WT	6	−1,556.9	3,126.1	26.71	0.00
4	Int + WT +WT^2 +AT + AT^2	8	−1,567	3,150.4	51.08	0.00
8	Int + WT + WT^2	6	−1,569.5	3,151.2	51.81	0.00
11	Int + WT + AT	6	−1,581.7	3,175.7	76.33	0.00
14	Int + WT	5	−1,582.9	3,175.9	76.55	0.00
7	Int + AT + AT^2	6	−1,588.2	3,188.5	89.15	0.00
15	Int + AT	5	−1,591.5	3,193.2	93.83	0.00
1	Int	4	−1,602.1	3,212.3	112.91	0.00

these activities predicted oviposition to occur before calling (Fig. 2). Part of this incongruence may be associated with our operational definition of onset date (when 5% of activity was complete). However, other factors that likely contributed to the unexpected and unreliable relationship between the timing of calling and oviposition include: coarse sampling of egg masses (weekly) compared to calling activity (daily), missed calling activity because we installed recording equipment after calling had already started, and equipment failures. Further, excessive background noise from high streamflows may have deterred males from calling or may have interfered with our detection of calls, especially in 1995 when streamflows were high. Using automated sound recording equipment to collect calling data may be an effective monitoring tool for this species. If calling occurs with some known timeframe before oviposition, managers could make real time flow adjustments or trigger flow ramping (the alteration of stream discharge resulting from dam operations) based on when calling is detected. Protective ramping of flows, therefore, could be underway prior to subsequent oviposition. Future work is needed to examine the relationship between these activities.

Stream Regulation and Climate Change.—Our findings suggest that stream water temperature and water depth strongly influence *R. boylii* calling and oviposition. Streamflow regulation from dams and changes in climate variables, such as snowpack and runoff regimes, can alter these two factors. Although streamflow thresholds that cue *R. boyii* breeding activities are site specific, it seems that a minimum threshold water temperature of near 10°C is required to initiate both calling and oviposition. Flow conditions at water temperatures above 10°C may be driving breeding activities. In 1994, calling and oviposition at the regulated MSTR site did not occur until water temperatures were well above 10°C because flow conditions were not suitable for breeding activity until late spring (end of May), when managers suppressed the amount of water released into the river (see Appendix 1). In the spring, controlled water releases on the MSTR maintain high flows and colder thermal regimes that benefit salmonids (Railsback et al., 2016). At the same time, these conditions delay or inhibit *R. boylii* breeding

TABLE 5. The linear mixed model set used to examine relationship of environmental variables to number of egg masses detected (response variable). Site and year were included as random factors in all models. df is the number of model degrees of freedom, logLik is the likelihood of the model, AICc is the corrected Akaike's information criterion, Δ_i is the difference in AICc between the top model and model *i*, ω_i is the Akaike weight for model *i* given the model set.

Model	Model structure [a]	df	logLik	AICc	Δ_i	ω_i
3	Int + Calls + Depth +Depth^2+AT +AT^2	9	−210.0	439.9	0	0.41
11	Int + Calls + Depth +AT	7	−212.7	440.6	0.69	0.29
13	Int + Calls + Depth +WT +AT	8	−212.3	442.2	2.28	0.131
15	Int + Calls + AT	6	−215.6	444.0	4.08	0.053
5	Int + Calls + Depth +Depth^2+WT +WT2 +AT +AT^2	11	−209.7	444.1	4.22	0.05
10	Int + Calls + Depth +WT +	7	−215.4	446.0	6.09	0.019
12	Int + Calls +WT +AT	7	−215.5	446.2	6.28	0.018
7	Int + Calls +AT +AT^2	7	−215.6	446.3	6.37	0.017
2	Int + Calls +Depth +Depth^2+WT +WT^2	9	−214.3	448.6	8.66	0.005
16	Int + Calls +WT	6	−218.3	449.4	9.49	0.004
4	Int + Calls +WT +WT^2 +AT +AT^2	9	−215.4	450.8	10.88	0.002
8	Int + Calls +WT +WT^2	7	−218.3	451.7	11.76	0.001
6	Int + Calls +Depth +Depth^2	7	−226.4	467.9	28.03	0
1	Int + Calls	5	−230.1	470.8	30.94	0
14	Int + Calls +Depth	6	−229.7	472.2	32.33	0
9	Int	4	−232.3	473.0	33.16	0

[a] Int indicates the intercept; Calls, weekly calling count; WT, weekly mean water temperature; AT, weekly mean air temperature.

activity and may have negative consequences on embryonic and tadpole development and tadpole growth (Wheeler et al., 2015; Railsback et al., 2016; Catenazzi and Kupferberg, 2017).

Based on predicted climate change models, California streams will become warmer, peak flows will occur earlier, summer flows will be lower, summer low flows will last longer, and amount of fall and winter rain and more frequent rain-on-snow events will augment discharge peaks (Power et al., 2015). Altered flow conditions because of climate-induced deviations in precipitation may impact some species, and warming temperatures and interactions with water-use demands for fisheries and agriculture may affect others (Dettinger et al., 2015). This study suggests that *R. boylii* breeding activity will be affected by changing environmental conditions, and our results may be useful in predicting how changes will impact this species. There are currently no published reports that indicate this species is breeding earlier with warming trends; however, zero reproductive success was documented at breeding sites in California that completely dried during consecutive severe drought years (S. Kuperferberg, pers. comm.). Low streamflows during drought years were associated with the expansion of the distribution of a nonnative predator of *R. boylii*, the American bullfrog (*Lithobates catesbeiana*), within a stream network, and bullfrog presence was a positive predictor of chytrid fungus (*Batrachochytrium dendrobatidis*) prevalence and load in *R. boylii* (Adams et al., 2017). Therefore, drier conditions attributed to climate change have likely already resulted in population-level lethal effects.

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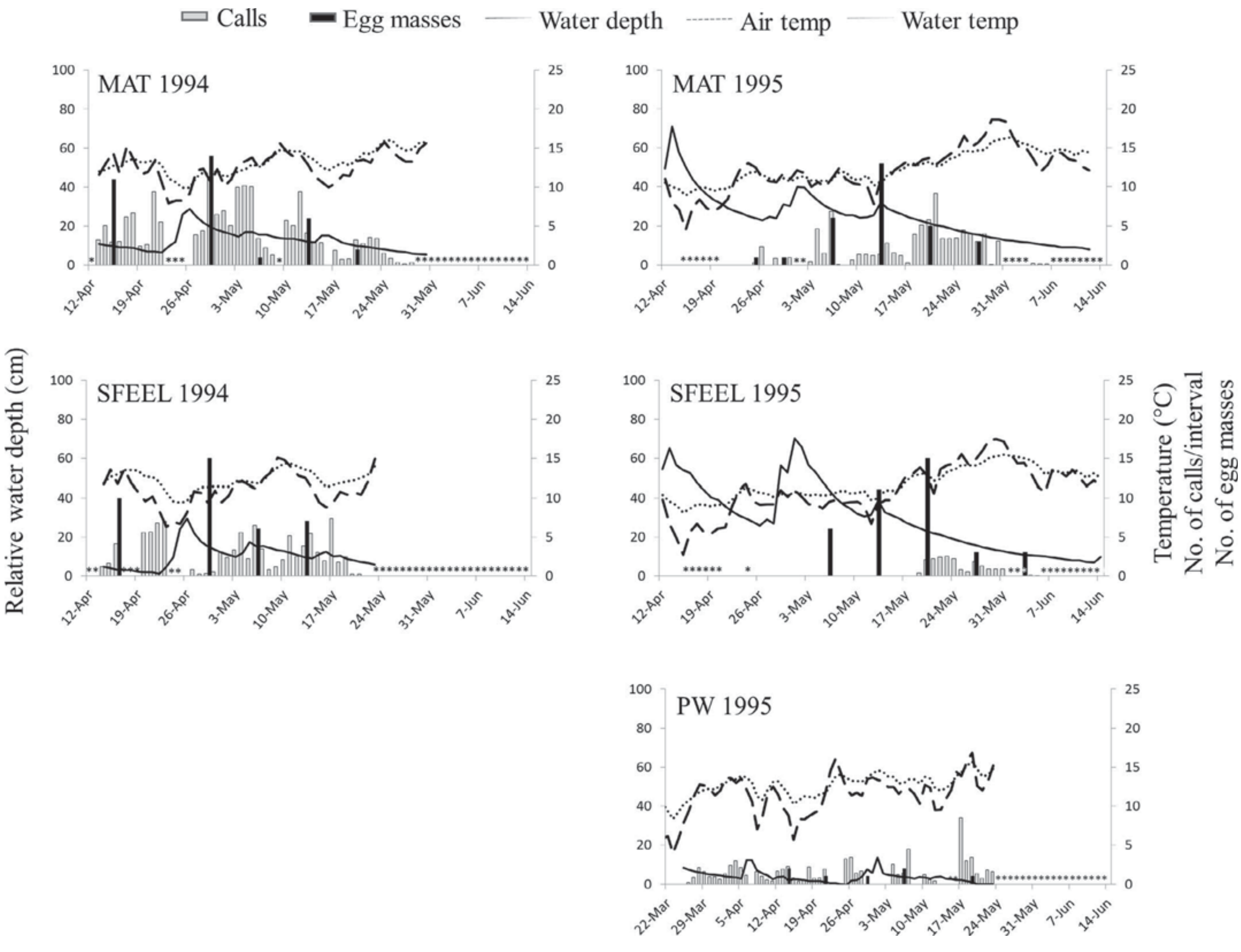
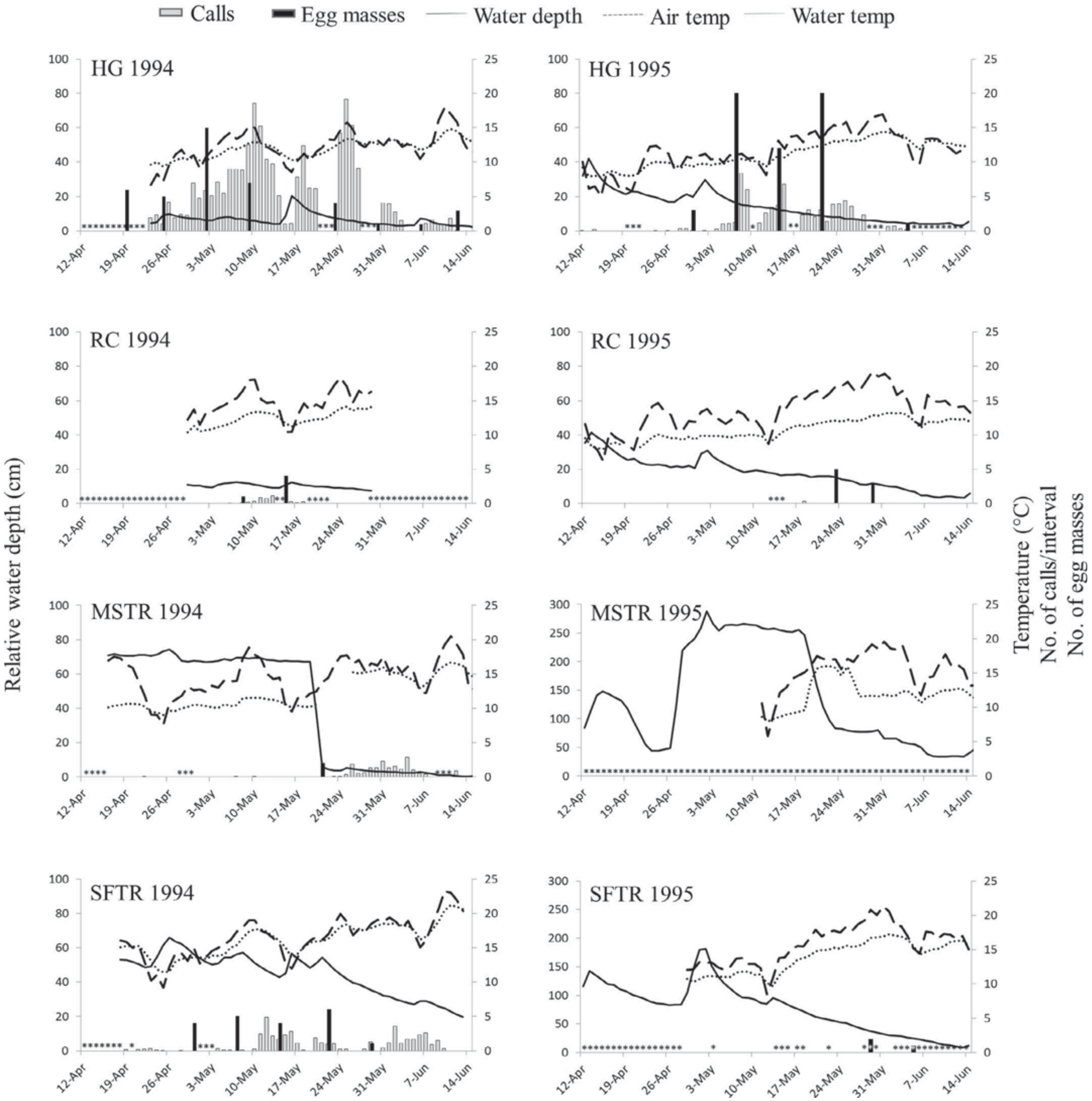


Appendix 1. Daily number of calls (per recording interval), weekly number of egg masses, water depth, air temperature, and water temperature at breeding sites in 1994 and 1995 in northwestern California, USA. Note: The water depth y-axis scale for MSTR 1995 and SFTR 1995 is not the same as other sites and years, and the date x-axis scale for PW 1995 is not the same as other sites and years.



APPENDIX 1. Continued.