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Modeling predicts that redd trampling by cattle may contribute to population declines of native trout

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Abstract. Unrestricted livestock grazing can degrade aquatic ecosystems, and its effects on native vertebrate species are generally mediated by changes to physical habitat. Recently, high estimated rates of cattle trampling on artificial redds within federal grazing allotments in southwestern Montana, USA, has raised concern that direct mortality from trampling may contribute to imperilment of native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*). To explore the implications of cattle trampling, we built two mathematical models. First we used a temperature-driven model of egg-to-fry mortality representative of the developmental stages during which embryos would be vulnerable to trampling. Cattle trampling was an additional source of mortality (beyond natural mortality), and we modeled egg-to-fry mortality across a range of trampling rates (25–125% per month) for scenarios assuming low (0.60), moderate (0.81), and high (0.95) natural mortality. We then used a matrix model to determine how trampling affected population growth (λ), assuming initially stable ($\lambda = 1.008$) or slow-growing populations ($\lambda = 1.025$ and 1.05). Cattle trampling concentrated over a few days when the embryos were most sensitive caused greater egg-to-fry mortality than when the same amount of trampling occurred over one month. Trampling caused a large increase in egg-to-fry mortality when that natural mortality was low, but the overall population-level effect was far less than might have been anticipated from the rate of trampling itself. Nonetheless, small reductions in population growth rate could be biologically significant for populations with little or no demographic resilience, and trampling rates as low as 25% could lead to negative population growth. The rapid reduction in resilience with increased trampling rates (>50%) means that even growing populations are less likely to recover from periodic fluctuations. The overall risk posed by trampling will depend on whether cutthroat trout populations face concurrent threats that have already reduced their abundance and resilience. Biologists can potentially use the egg-to-fry model and thermograph data to identify dates when limiting cattle presence in or near stream habitats would likely reduce mortality from trampling. Evaluation of grazing policies on federal lands may be needed to ensure that species conservation and land use concerns are equitably balanced.

Key words: cattle grazing; mechanical disturbance; Montana, USA; mortality; Oncorhynchus clarkii lewisi; *persistence; population models; resilience; riparian habitat; trampling; westslope cutthroat trout.*

INTRODUCTION

In the arid and semiarid landscapes of the western United States, grazing by domestic livestock has long been seen as an important influence on the integrity of terrestrial and aquatic ecosystems. Livestock grazing can fundamentally alter ecological processes and the structure, pattern, and resilience of vegetative communities (Ludwig et al. 1997, Fuhlendorf and Engle 2001). Considerable effort has been focused on the effects of grazing on the composition and density of riparian vegetation because of the subsequent indirect effects on riparian and aquatic species. For example, grazing may result in a loss of stability, shading, and habitat complexity in stream channels (Platts 1991, Rinne 1999), increased erosion and fine-sediment deposition (Platts 1991, Armour et al. 1994, Belsky et al. 1999), disruption of stream food webs (Saunders and Fausch 2007) and, ultimately, survival and abundance of aquatic vertebrates (Binns and Remmick 1994). Livestock grazing is also known to cause direct mortality of terrestrial organisms through trampling (Guthery and Bingham 1996, Bates et al. 2007, Adams et al. 2009) and may be important for fishes and other organisms that incubate their embryos in stream gravels (Gregory and Gamett 2009). Despite the substantial

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TABLE 1. Mortality rates for cutthroat trout (*Oncorhynchus clarkii lewisi*) embryos experiencing natural ($Z_{\mathrm{NT},i}$) and trampling mortality ($Z_{\mathrm{TR},i}$) during five developmental stages within federal grazing allotments in southwestern Montana, USA.

Stage (i)	Cumulative CTU	Total CTU	$Z_{\mathrm{TR},i}$	Total finite mortality rates, $Z_{\mathrm{NT},i}$ 0.60	0.81	0.95	Total Z_{NT} per stage (%)
Green egg	0–175	175	0.041	0.084	0.153	0.276	9.22
Eyed egg (part 1)	176–260	85	0.066	0.035	0.064	0.115	3.85
Eyed egg (part 2)	261–300	40	0.556	0.154	0.280	0.504	16.84
Hatching	301–330	30	0.368	0.258	0.467	0.843	28.14
Preemergent sac fry	331–500	170	0.210	0.384	0.697	1.257	41.96

Notes: Columns 4–7 show stage-specific (i) instantaneous mortality rates for embryos associated with individual trampled redds (Z_{TR}) and instantaneous natural mortality rates (Z_{NT}) for total finite mortalities of 0.60, 0.81, and 0.95. Celsius temperature units (CTU) are the sum of mean daily temperature in degrees Celsius.

body of literature focused on the indirect effects of livestock to stream ecosystems, however, relatively little information exists on the possible role of direct mortalities caused by cattle. This may be a particularly important issue for remnant populations of native fishes that overlap with cattle grazing during a critical portion of their life cycle.

Cattle have a propensity to congregate in riparian habitats and frequently wade through streams during warm weather (Armour et al. 1994, Fleischner 1994). These behaviors have the potential to affect populations of spring- and summer-spawning cutthroat trout (*Oncorhynchus clarkii*), whose developing embryos can remain in stream gravels until late summer or early fall. Trout embryos are vulnerable to mechanical disturbance, and their sensitivity varies with developmental stage (Jensen and Alderdice 1983, Johnson et al. 1983, Roberts and White 1992). Mortality from the direct crushing or physical disturbance of trout embryos can be substantial. For example, Roberts and White (1992) conducted a set of laboratory experiments to measure effects of angler wading and found that twice-daily wading throughout embryo development killed at least 83% of eggs and pre-emergent fry of three trout species.

Trampling of simulated trout redds (clay targets or pigeons) in streams on two national forests indicates that cattle could have comparable effects. In both cases, the frequency of cattle trampling was estimated by comparing trampling rates in the presence or absence of cattle, where absence provided a control to estimate trampling by wild ungulates and simulated redds were placed in suitable spawning habitat within randomly selected study reaches (Gregory and Gamett 2009; J. A. Brammer, *unpublished data*). On average, cattle trampled 50% of simulated cutthroat trout redds (and wild ungulates trampled 19%) over a ~30-d grazing period for trials conducted over two years in 17 randomly selected streams within grazed allotments across six ranger districts on the Beaverhead-Deerlodge National Forest, Montana (J. A. Brammer, *unpublished data*). Stream reaches were primarily small (mean width ~2 m at base flow), low gradient (<2%), with riparian zones dominated by grass and deciduous shrubs. Similarly, Gregory and Gamett (2009) estimated that cattle affected 12–78% of simulated bull trout (*Salvelinus confluentus*) redds during a 14–21-day grazing period in three streams on the Salmon-Challis National Forest, Idaho. These data raise the concern that cattle trampling may be a significant source of mortality for native fishes in some streams. The issue may be particularly acute where populations face concurrent threats from nonnative fish species or habitat degradation. Whether cattle trampling results in egg-to-fry mortality sufficient to cause declines in wild populations, however, has not been evaluated.

Our goal was to estimate and model the effects of trampling by cattle on egg-to-fry mortality for stream-resident cutthroat trout and to explore the demographic implications of that mortality. We used results of Roberts and White (1992) to estimate the mortality caused by cattle trampling and incorporated these estimates into a temperature-driven model of egg-to-fry mortality representative of the developmental stages during which resident cutthroat trout populations in central and southwestern Montana would be vulnerable to the effects of trampling by cattle. The egg-to-fry model was used to characterize the effects of trampling by cattle in streams under two thermal regimes and across a range of empirically estimated trampling rates from typical cattle grazing scenarios. We linked the egg-to-fry model to a matrix population model to evaluate how trampling affects population growth rates, then considered how trampling may influence persistence in demographically isolated populations.

METHODS

Egg-to-fry mortality

Westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) spawn in late spring or early summer (McIntyre and Rieman 1995, Magee et al. 1996), and development from fertilization to emergence requires ~500 Celsius temperature units (CTU; the sum of mean daily temperature in degrees Celsius; Behnke 1992, Roberts and White 1992). The embryos develop through a progression of developmental stages based on the accumulated temperature units, and these stages differ in their sensitivity to mechanical disturbance (Roberts and White 1992). We defined five discrete stages (Table 1) and estimated the stage-specific effects of redd

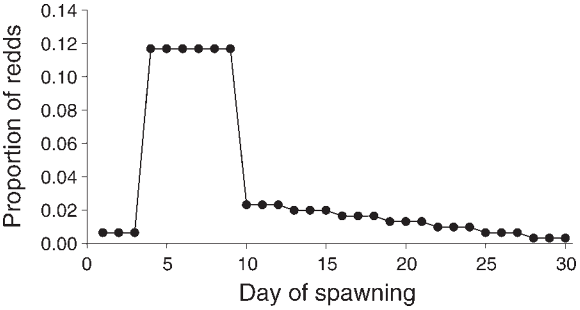

FIG. 1. Assumed spawning distribution of stream-resident cutthroat trout (*Oncorhynchus clarkii lewisi*) used to model the effects of redd trampling in southwestern Montana, USA. We used a simple function to describe the proportion of redds created (i.e., eggs deposited and fertilized) on each day during a 30-d spawning period.

trampling using experimental data for cutthroat trout and related salmonids (Roberts 1988, Roberts and White 1992).

We assumed a type 2 mortality model (Ricker 1975) and treated redd trampling as additional mortality analogous to competing fishery-related mortality. Stage-specific (i) finite mortality (A_i) in the presence of a single trampling event is

$$A_i = M_i + T_i - M_i T_i \tag{1}$$

where M_i is natural mortality (in the absence of cattle trampling) and T_i is cattle trampling mortality (Ricker 1975). Algebraic rearrangement of Eq. 1 yields

$$T_i = \frac{A_i - M_i}{1 - M_i} \tag{2}$$

which we used to calculate T_i using estimates of A_i and M_i from Roberts (1988) and Roberts and White (1992). Stage-specific finite mortality from trampling was transformed to instantaneous mortality as $Z_{\mathrm{TR,i}} = -\ln(1 - T_i)$. Total finite mortality in the absence of trampling (M) was similarly transformed to instantaneous mortality (Z_{NT}) and subsequently partitioned into stage-specific instantaneous natural mortality ($Z_{\mathrm{NT},i}$) based on the distribution of instantaneous mortality presented in Table 1 (see Appendix A for derivation). Thus, total instantaneous mortality is

$$Z_{\mathrm{TOT}} = \sum_{i=1}^{n} (Z_{\mathrm{NT},i} + Z_{\mathrm{TR},i}) \tag{3}$$

for the $n = 5$ stages (Table 1).

Data from streams in southwestern Montana indicate that the initiation of spawning in resident cutthroat trout is correlated with the date when water temperatures reach ~8°C, and spawning generally lasts ~30 d, with most redds constructed in the first 7–10 d (Magee 1993, Magee et al. 1996). We used 8°C as the model's thermal trigger for reproduction and created a function describing the temporal distribution of redd contruction during the 30-d spawning period (Fig. 1). Approximately 75% of redds were created during days 4–11. Our default function was right-skewed, but the model can accommodate alternative spawning distributions (e.g., normal or uniform). We defined a cohort as a group of individuals that were spawned on a particular day, so our model population had 30 separate egg-to-fry cohorts whose development could be followed in daily increments.

Stream temperatures are fundamental to modeling developmental rates and stage-specific mortality. To create representative stream temperature regimes we used nonlinear regression to model stream temperature based on 100 mean daily temperatures (for 16 June to 23 September 2006) from two thermographs in Jack Creek in southwestern Montana (Fig. 2a). Jack Creek is a small stream in the upper Missouri River basin, and at the lower thermograph location (46°21′48″ N, 112°18′16″ W, elevation 2009 m) the stream had a mean wetted width of 1.67 m and a drainage area of 588 ha. We were interested in general developmental response to temperature because this controlled stage of development and sensitivity of cutthroat trout embryos to

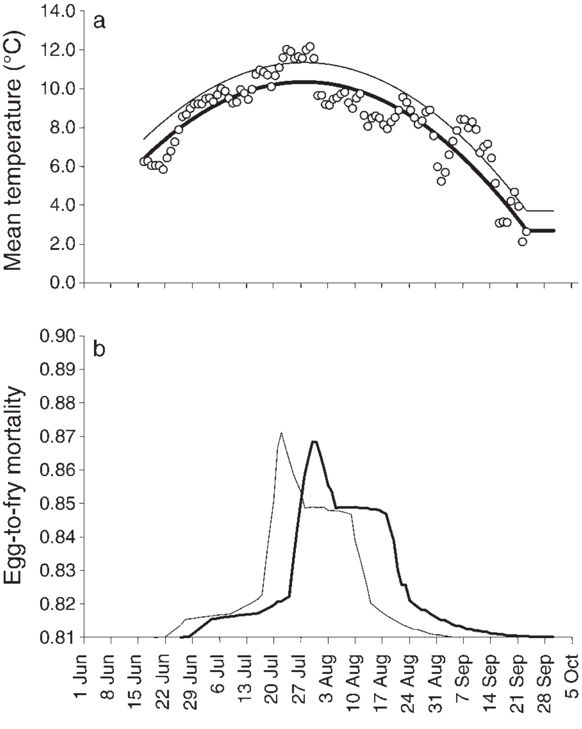

FIG. 2. (a) Actual and modeled water temperatures used to model the effects of redd trampling in southwestern Montana and (b) sensitivity of total egg-to-fry mortality to mean summer water temperature given 100% trampling on that day. In panel (a), open circles are mean daily temperatures in Jack Creek (see *Methods: Egg-to-fry mortality*). Line plots represent (a) modeled temperatures or (b) mortality for streams with 9.6°C (thick line) or 10.6°C (thin line) as the mean summer water temperature during July and August. In panel (b) we assumed a natural mortality of 0.81 and the spawn timing distribution shown in Fig. 1.

trampling. For that reason we fit a quadratic function that predicted a smooth temperature pattern (either steadily increasing or decreasing relative to the maximum summer temperature), rather than a more complex function that might reflect daily variations (Fig. 2a).

The modeled mean daily July–August temperatures were equivalent to those in Jack Creek (both 9.6°C), and the accumulated CTU differed little (model 593.9 CTU, Jack Creek 597.4 CTU for July–August). The regression equation $6.212 + 0.1952(\text{day of year} - 166) - 0.0023(\text{day of year} - 166)^2$ ($\text{df} = 2$, $P < 0.001$, $R^2 = 0.79$) was used to predict temperatures from 16 June to 23 September, whereas the mean daily temperature during 24–31 September was held constant at 2.7°C (the predicted daily mean temperature on 23 September). The predictions were truncated and temperature held constant during the final week of the stream profile because the regression equation predicted a decline to 0°C, which would be unrealistic except in the case of an early winter storm. Rather, we assumed that temperature would decline little more until the actual onset of winter. This assumption was unlikely to strongly influence overall mortality as 28 of 30 simulated trout cohorts emerged by 23 September when summer mean temperature was 9.6°C. To explore the biological response to temperature variation, we generated a warmer thermal regime by adding 1°C to the corresponding daily estimate for the colder regime. The warmer thermal regime (mean daily July–August temperature = 10.6°C) accumulated 655.9 CTU for the 100-d period.

To calculate the instantaneous mortality for each of the 30 cohorts, we partitioned the total instantaneous mortality for a given stage into daily increments based on the CTU accumulated per day. For example, we defined the preemergent sac fry stage as lasting 170 CTU (Table 1), and, for a wild population with 0.81 natural egg-to-fry mortality, the estimated instantaneous natural and trampling mortalities for the stage are 0.697 and 0.210, respectively. Thus, if the mean daily temperature was 10°C, then the proportion of instantaneous natural mortality that occurs on that day was: $(0.697) \times (10/170) = 0.041$. Within a developmental stage daily natural mortality was assumed to accrue at a constant rate. Trampling mortality, if any, was similarly calculated based on the proportion or percentage of redds trampled on that date, but with two provisions. First, the total instantaneous trampling mortality per stage could not exceed the values in Table 1, as those trampling mortalities were estimated from a single wading event in each developmental stage (Appendix A). Second, the maximum trampling effect for a given stage could occur within one day if all redds were trampled on that day. If half the redds were trampled (trampling rate 50%), then the corresponding daily instantaneous trampling mortality would be $0.5 \times 0.210 = 0.105$. If the same amount of trampling was repeated on the next day, then the stage-specific total would have been reached (i.e., $0.105 + 0.105 = 0.210$) and no more additional trampling mortality would accrue during that stage. In effect, the model could estimate the effect of multiple trampling events across, but not within, developmental stages. The two sources of mortality were subsequently totaled by stage and cohort. The population-level instantaneous egg-to-fry mortality was estimated from a weighted average across cohorts based on the proportion of redds that a cohort contributed to the population (see Fig. 1).

To characterize temporal sensitivity to trampling, we modeled total egg-to-fry mortality by assuming all redds were trampled on a single day for each day of the incubation period. We then modeled a range of trampling rates that bounded observed estimates from artificial redds (J. A. Brammer, *unpublished data*) for calendar dates of deferred and rest-rotation grazing regimes typical of those in National Forest allotments in the Beaverhead-Deerlodge National Forest. The observed mean monthly cattle trampling rate was ~50%, which meant that half the redds present were trampled at least once by cattle during that time. For modeling and inference, we consider this value representative of mean trampling rates on westslope cutthroat trout redds for populations within grazing allotments in southwestern Montana. To bound the mean value, we modeled trampling rates from 25% to 125% per 30 d (0.83–4.17%/d). We modeled five different grazing regimes: month-long grazing beginning in (1) July, (2) August, or (3) September, (4) grazing 1 July to 15 August, and (5) grazing 16 August to 30 September. The spatial distribution of redds and trampling was assumed to be random. Given uncertainty about egg-to-fry mortality rates in wild populations (e.g., Shepard et al. 1997, Peterson et al. 2008*b*), we modeled natural mortality rates from 0.60 to 0.95 for all trampling rates and grazing durations. The egg-to-fry mortality model was implemented with an Excel spreadsheet (version 2003).

Population effects

To evaluate potential population-level effects of trampling, we incorporated egg-to-fry mortalities into an overall demographic model (e.g., Morris and Doak 2002) for stream-resident cutthroat trout. We developed a six-stage birth pulse matrix population model for westslope cutthroat trout based on length–frequency data from southwestern Montana, and age- and length-at-maturity and a fecundity-at-length regression equation from similar populations (Appendix B). We modeled females only, assuming that fish were age 3 yr (≥150 mm fork length [FL]) at age of first reproduction and spawned in alternate years after initial maturity. Values for mortality of trout age 0 and older were estimated as the midpoint in the range of values used in other models for similar species and environments (Table 2 and Appendix B). Egg-to-fry mortality in the absence of trampling was estimated by default (0.81) as the value required to achieve a stable population ($\lambda = 1.008$) after selecting all other vital rates. We did this because egg-to-fry mortality is difficult to measure in

TABLE 2. Demographic parameters for three cutthroat trout population scenarios with different egg-to-fry mortalities used to model trampling effects.

Demographic parameter or rate	Population scenario (egg-to-fry mortality)† High	Moderate (default)	Low
Survival			
Egg-to-fry	0.050	0.190	0.400
Age 0	0.363‡	0.277	0.234‡
Age 1 yr	0.447‡	0.341	0.288‡
Age 2 yr and older	0.613‡	0.468	0.395‡
Reproductive output			
Age 3 yr (small adult, 150–175 mm FL)§	1.38	5.23	11.01
Age 4 yr (medium adult, 175–200 mm FL)§	4.74	18.00	37.90
Age 5 yr (large adult, 200–250 mm FL)§	6.46	24.55	51.69
Matrix model population growth rate (λ)	1.008	1.008	1.008

Notes: For each scenario, the combination of demographic parameters produces a stable population (λ = 1.008) under the general matrix model (Appendix B). Moderate egg-to-fry mortality 0.810 (survival = 0.190) was the default scenario. Egg-to-fry mortalities for high- and low-mortality scenarios were based on maximum and minimum values reported in the literature, and the other model parameters were adjusted to produce a stable population.

† Fishery models such as the one we adapted to characterize egg-to-fry development generally consider mortality, but demographic models typically use survival to represent transitions between age classes or life history stages. We use both terms depending on the application, but they convey the same information and can be directly calculated from one another.

‡ Values are based on adjusting corresponding rates in the moderate egg-to-fry mortality (default) population scenario by a factor of 1.312 (high egg-to-fry mortality scenario) or 0.8445 (low egg-to-fry mortality scenario).

§ Calculations for reproductive output are presented in Appendix B. FL stands for fork length.

wild cutthroat trout populations, and the range of assumed values can be large (e.g., Shepard et al. 1997). We qualitatively characterized this default egg-to-fry mortality rate (0.81) as moderate.

To consider variation or uncertainty in egg-to-fry mortality among populations, we generated two additional population scenarios that assumed either high (0.95) or low egg-to-fry mortality (0.60) that, in combination with mortality rates at other stages, also resulted in a stable population (λ ~ 1.008). To achieve this we adjusted the mean mortality rates for ages 0 and older used in the moderate-mortality scenario, under the assumption that those other rates must either increase or decrease to compensate for high or low egg-to-fry mortality.

To explore the consequences of trampling in populations that may have some modest capacity to buffer additional embryo mortality, we also modeled populations with 2.5% and 5.0% annual growth (λ = 1.025 or 1.050) under each scenario. We did this by assuming egg-to-fry mortality drives population growth and reduced this rate to achieve the desired λ in the absence of trampling.

Overall, we had nine scenarios for which we considered the population-level consequences of redd trampling based on the combinations of three egg-to-fry mortality rates and three population growth rates. For all nine combinations, we assessed the effect of trampling on population growth rates for a subset of grazing and temperature conditions, typically month-long grazing in August for a stream with mean summer temperature 9.6°C. In contrast to monthly or longer grazing regimes, we also explored the consequence of higher trampling rates (8–10%/d) over a shorter duration (5–10 d) that was consistent with observations in at least one stream (J. A. Brammer, *unpublished data*). The matrix population models were implemented in Excel using the PopTools add-in feature (Hood 2008).

Because of the competing effects of natural and trampling-induced embryo mortality, the effects of trampling estimated as absolute changes in λ may be relatively small when natural mortality is high. Small changes, however, may influence the resilience of populations in variable environments. In a final analysis, we considered how trampling might influence doubling time and the persistence of small, demographically isolated cutthroat trout populations given the observed λ and plausible environmental variation, respectively. Doubling time was simply the time necessary to double the total population number, given the λ associated with a specific trampling scenario. We estimated the probability of persistence with the diffusion approximation method of Dennis et al. (1991) implemented with program StochMVP (E. O. Garton, *personal communication*). These simulations assumed an initial population size of 1000 (~200 adults), a quasi-extinction threshold of 100 individuals (~20 adults; McIntyre and Rieman 1995), a variance in instantaneous population growth of 0.4, and a time horizon of 20 years (see also Peterson et al. 2008*b*).

RESULTS

Egg-to-fry mortality

As expected, the different thermal profiles led to differences in the timing and duration of greatest

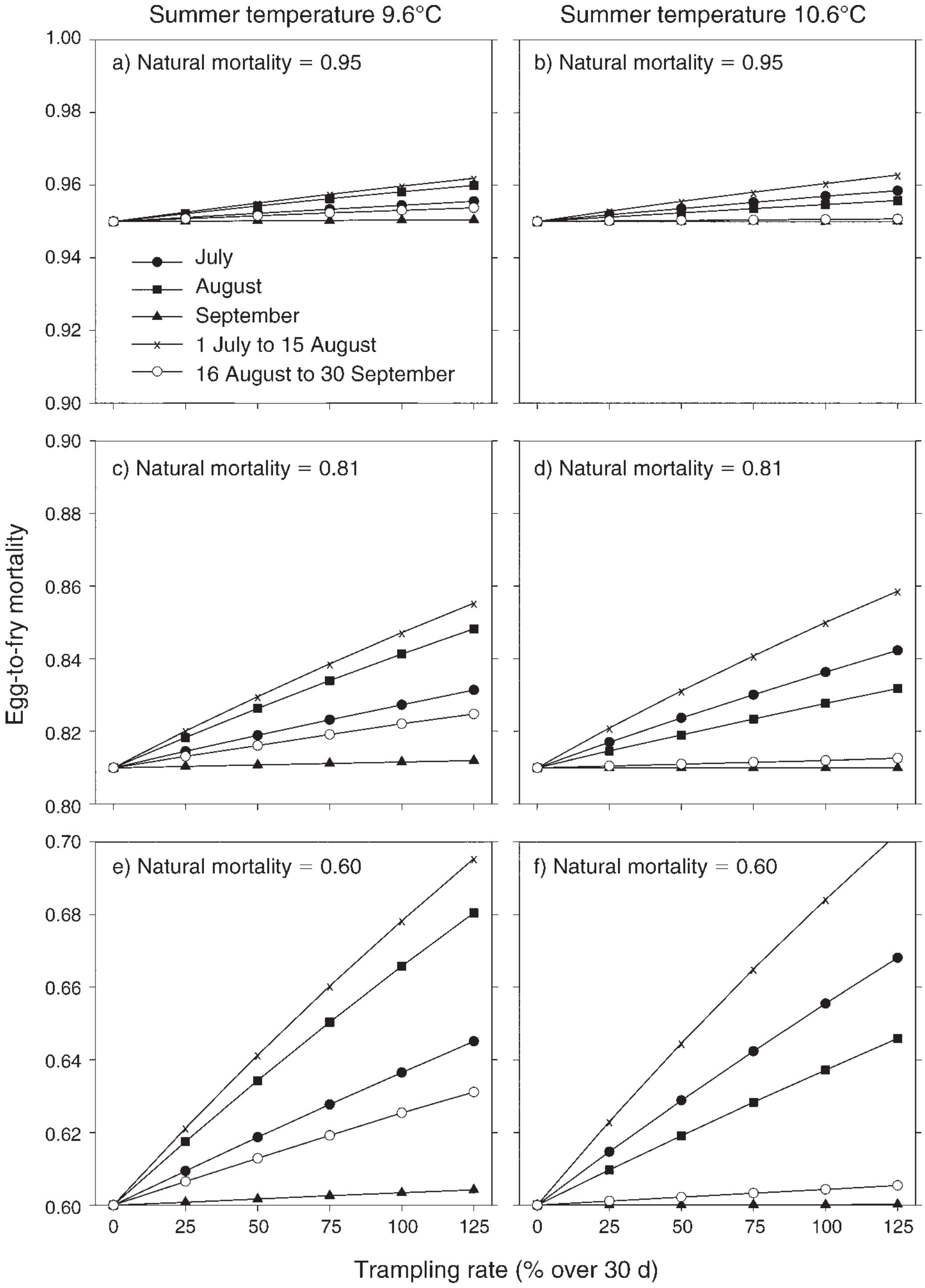

FIG. 3. Total egg-to-fry mortality relative to mean summer temperature, natural mortality, grazing regime, and trampling rate. Plots present effects of four different grazing regimes assuming natural egg-to-fry mortality rates of (a, b) 0.95, (c, d) 0.81, and (e, f) 0.60. Note that *y*-axes have different absolute values but the same scaling and range.

sensitivity to trampling (Fig. 2b). Assuming natural mortality was 0.81, the general pattern of sensitivity was similar between the two profiles; however, peak sensitivity was 9 d later and the duration of elevated sensitivity was longer for colder water temperatures (Fig. 2b). Complete trampling resulted in total egg-to-fry mortality >0.815 for each of 30 d (26 July to 24 August) in the colder stream compared to 27 d (18 July to 14 August) in the warmer stream. A normal, instead of the default right-skewed, spawning distribution resulted in effects of equal magnitude but with a shift in the timing of that mortality (D. P. Peterson, *unpublished data*).

Total egg-to-fry mortality increased with trampling rate and grazing duration, but there was relatively little additional trampling-related mortality when natural mortality rates were high (Fig. 3). For example, if on average each redd was trampled once, during August

TABLE 3. Egg-to-fry mortality and population growth rate for stream-resident cutthroat trout for two temperature regimes across a range of 30-d trampling rates (25–125%) for five grazing regimes.

Grazing regime	Duration (d)	Temperature regime (°C)†	Egg-to-fry mortality					Deterministic population growth rate				
			25%	50%	75%	100%	125%	25%	50%	75%	100%	125%
July	31	9.6	0.812	0.819	0.823	0.827	0.831	1.007	1.000	0.995	0.991	0.987
		10.6	0.817	0.824	0.830	0.836	0.842	1.001	0.995	0.988	0.982	0.975
August	31	9.6	0.818	0.826	0.834	0.841	0.848	1.000	0.992	0.984	0.976	0.969
		10.6	0.815	0.819	0.823	0.828	0.832	1.004	0.999	0.995	0.991	0.986
September	30	9.6	0.810	0.811	0.811	0.812	0.812	1.008	1.007	1.007	1.007	1.006
		10.6	0.810	0.810	0.810	0.810	0.810	1.008	1.008	1.008	1.008	1.008
1 July to 15 August	46	9.6	0.820	0.830	0.839	0.847	0.855	0.998	0.989	0.979	0.970	0.960
		10.6	0.821	0.831	0.841	0.850	0.859	0.997	0.987	0.977	0.966	0.956
16 August to 30 September	46	9.6	0.813	0.816	0.819	0.822	0.825	1.005	1.002	1.002	0.996	0.994
		10.6	0.811	0.811	0.812	0.812	0.813	1.008	1.007	1.007	1.006	1.006

Note: Results are for the moderate egg-to-fry mortality scenario (0.81) with $\lambda = 1.008$ in the absence of trampling, and $\lambda < 1.0$ indicates populations predicted to decline.

† Mean summer (July–August) temperature.

under the cold thermal regime when natural mortality was 0.95, then mortality increased to ~0.96 (Fig. 3a). If natural mortality was 0.60, then mortality increased to ~0.67 under the same trampling (Fig. 3e). Small changes in total mortality, however, were equivalent to large relative changes in survival. Increasing mortality from 0.95 to 0.96 and from 0.60 to 0.67 represented a 20% and 17.5% relative decrease in survival, respectively.

The effects under a given grazing regime and trampling rate varied with water temperature. For month-long grazing scenarios, mortality with colder temperatures (9.6°C) was greatest for August, whereas with warmer temperatures (10.6°C) it was highest during July (Fig. 3). Longer-duration early-season grazing (1 July to 15 August) resulted in the highest mortalities, regardless of temperature. Trampling in September had little effect.

Population-level effects

Assuming moderate egg-to-fry mortality, the deterministic population model predicted that if the cumulative 30-d trampling rate was at least 50%, then in five of six cases for trampling during July, August, or July through mid-August the population would decline ($\lambda < 1$) (Table 3). The effect was small, however, and λ averaged 0.992 for these five cases. If the trampling rate increased to 125% (each redd trampled 1.25 times on average, over 30 d), then all six cases resulted in $\lambda < 1$, with an average of 0.972.

Across the three population scenarios, larger absolute increases in egg-to-fry mortality were needed to produce an equivalent change in λ when natural mortality was lower (Figs. 3 and 4). Initial $\lambda \geq 1.025$ provided limited buffering (Fig. 4). The trampling effect was qualitatively similar (i.e., slope) across the three scenarios (Fig. 4), but the estimates of λ dropped below 1 only in the worst cases as the pre-trampling λ increased. Worst-case scenarios of trampling concentrated during sensitive periods of embryo development resulted in larger decreases in λ relative to the same amount of trampling distributed over a longer time period (Fig. 5). Doubling time increased rapidly with increased trampling. For a population with 200 adults, the probability of persistence was 0.70 and declined substantially and linearly with increased trampling (Fig. 6).

DISCUSSION

The egg-to-fry mortality and matrix population models showed that cattle trampling could contribute important additional mortality to cutthroat trout populations. The overall effect depended on the timing and rate of trampling and the population's demographic characteristics. High cattle trampling rates did not necessarily lead to dramatic changes in population trajectory. Trampling may add relatively little to total mortality when natural mortality is already high. In general, trampling was not expected to cause rapid population declines, but it did erode population resiliency and could lead to deterministic declines in certain situations.

Trampling during the most sensitive developmental stages can lead to mortality and population-level effects disproportionate to the total number of redds disturbed. By design, the hatching and latter part of the eyed-egg stage were most sensitive to disturbance (see Table 1), but the overall effect of trampling concentrated when the largest cohorts were in these stages was striking. Trampling 75% of vulnerable redds in August reduced λ from 1.05 to 1.025; but if 75% of the redds were trampled during a 5- or 10-d period when the largest cohorts of embryos were most sensitive to disturbance, then λ decreased to 1.00 or 1.01, respectively. Intense, short-duration trampling has been observed with simulated redds (J. A. Brammer, *unpublished data*) and should be considered an important concern for trout along with more chronic effects. The effects of short-duration vs. continuous grazing may be different for terrestrial species (Koerth et al. 1983, Guthery and Bingham 1996).

Increased egg-to-fry mortality caused by trampling generally caused small reductions in λ, but these effects could still be biologically significant for populations

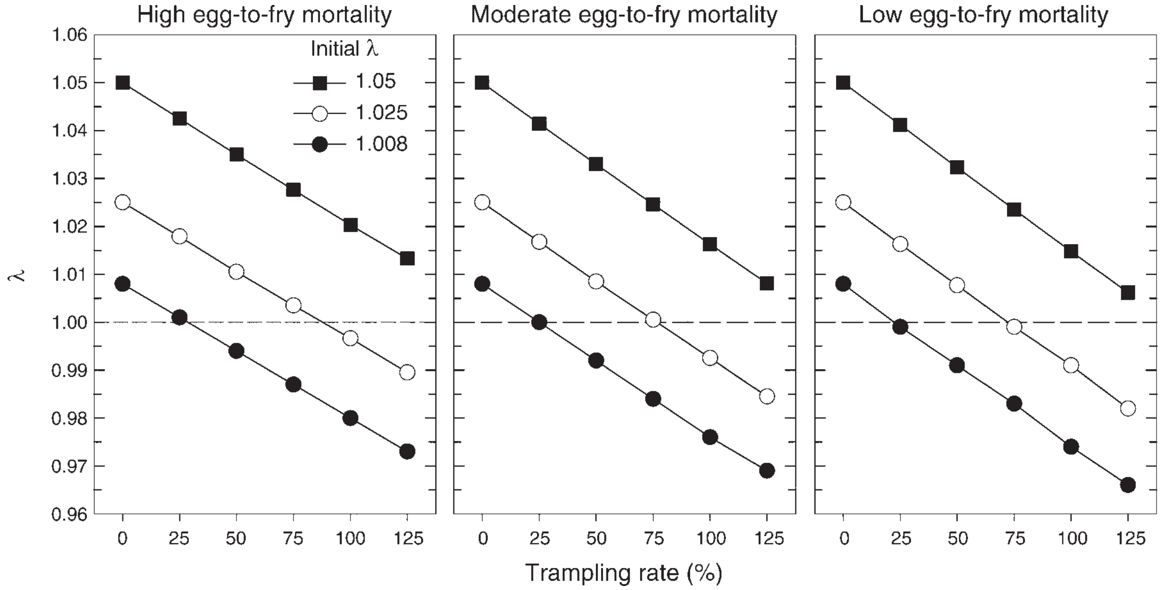

FIG. 4. Population growth rate (λ) in response to month-long cattle trampling in August for three representative population scenarios with high, moderate, and low natural egg-to-fry mortality rates and λ = 1.008, 1.025, and 1.05 in the absence of trampling. Higher λ values were used to represent populations with some capacity to buffer the effects of additional trampling mortality. Points below the dashed horizontal line at λ = 1.00 represent declining populations.

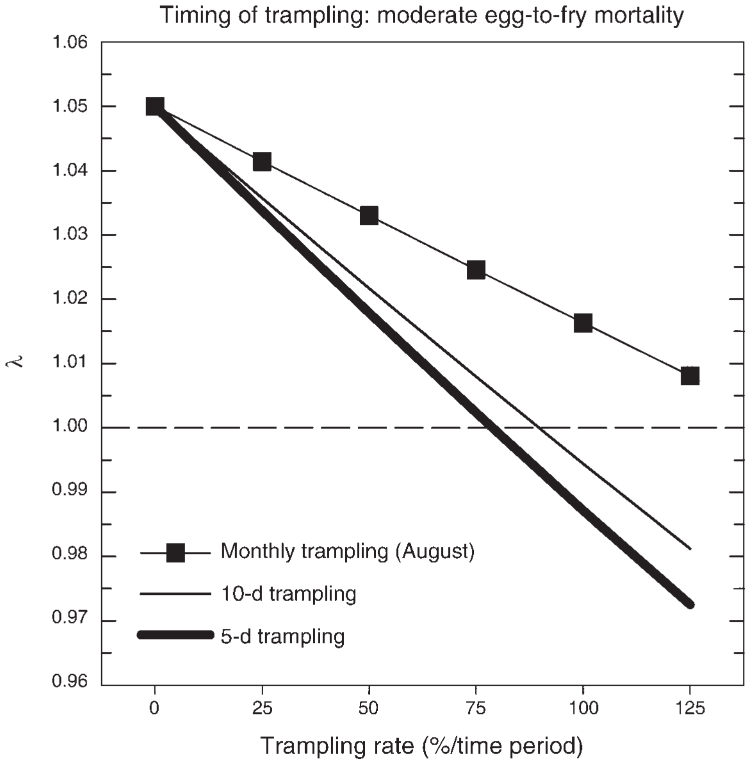

FIG. 5. Population growth rate (λ) in response to chronic vs. short-duration, high-intensity trampling. The total trampling rate was constant but distributed across a one-month period (August; i.e., chronic trampling) or across 5-d and 10-d periods during which embryos were most sensitive to mechanical disturbance (29 July–2 August and 27 July–5 August, respectively). We assumed 9.6°C mean summer water temperature and moderate egg-to-fry mortality producing λ = 1.05 in the absence of trampling.

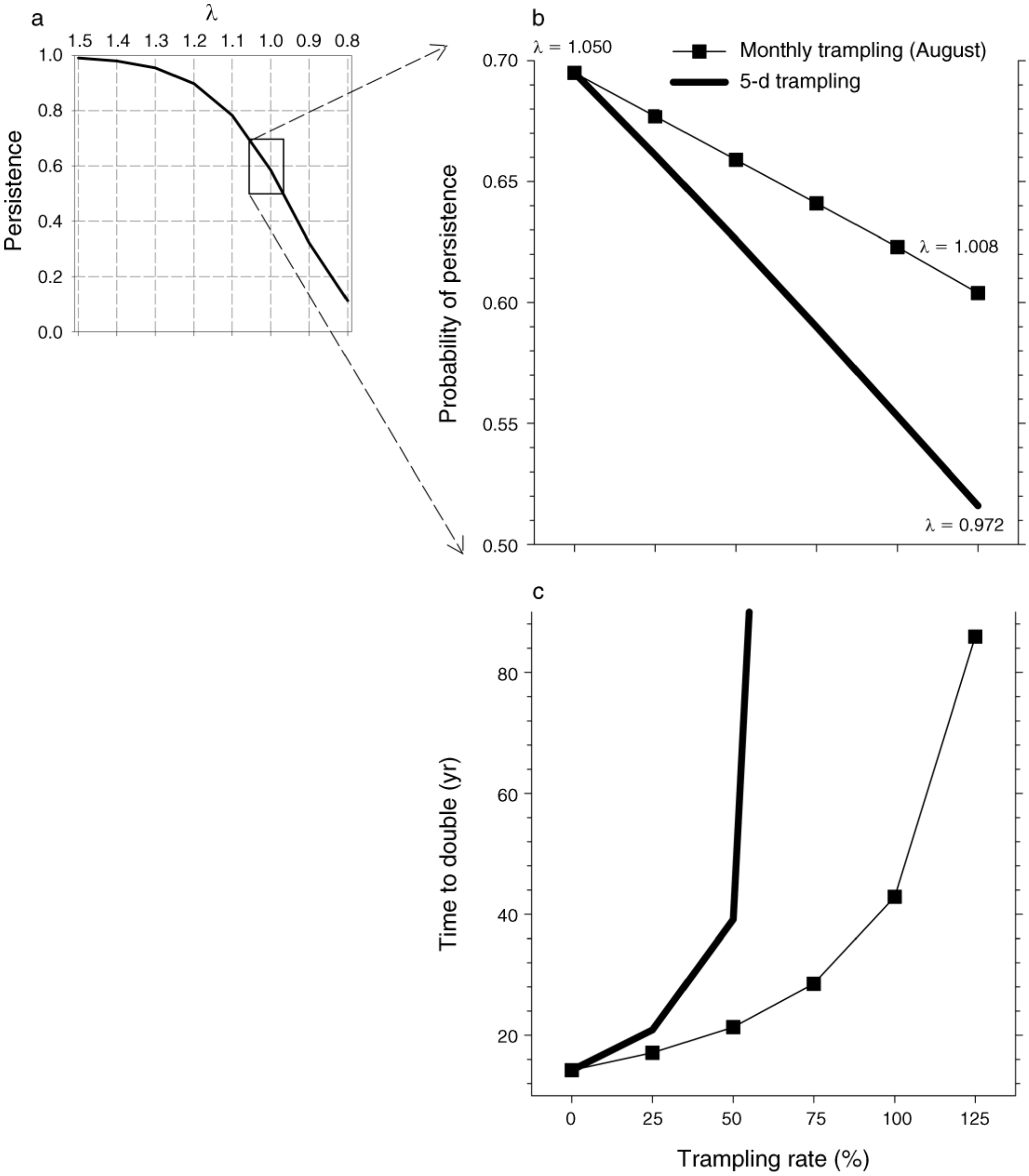

FIG. 6. Effect of trampling on the probability of persistence for a hypothetical population of stream-resident cutthroat trout. (a) The relationship between λ and the 20-yr probability of persistence for a starting population of 1000 individuals age 1 yr and older, variance in instantaneous growth rate of 0.4, and quasi-extinction threshold of 100 individuals (~20 adults) using the diffusion approximation method (e.g., Rieman and McIntyre 1993). (b, c) For a subset of populations with $\lambda = 1.05$ in the absence of trampling, the effect of different trampling rates on the 20-yr probability of persistence and population doubling time given a constant trampling rate distributed across August and across the 5-d period most sensitive to trampling (see Fig. 5). We assumed 9.6°C as mean summer water temperature.

with little or no demographic resilience. Our results indicate that, depending on the inherent resilience (or underlying population growth rate), trampling rates as low as 25% could lead to negative population growth and, presumably if unchecked, toward extirpation. Cattle trampling estimates based on simulated redds ranged from 41% over 2–3 weeks (Gregory and Gamett 2009) to 50% over 1 month (J. A. Brammer, *unpublished data*) and potentially even higher if intense grazing coincides with embryo vulnerability. For more resilient populations higher trampling rates than those we modeled are required to reduce population growth rates below 1.0, but even positive growth rates do not ensure persistence for small, isolated populations in variable environments (McIntyre and Rieman 1995, Hilderbrand and Kershner 2000). The rapid reduction in resilience with increased trampling rates in our scenarios essentially means that populations are increasingly less likely to recover from periodic fluctuations that may well be part of any natural system or to respond to management that does not address grazing effects. We do not have precise estimates of the inherent λ for cutthroat trout populations associated with the grazing studies considered here and we also have a limited understanding of natural variability. Our estimates are simply first approximations given the available information (e.g., McIntyre and Rieman 1995).

We anticipate, then, that the overall risk posed by trampling will depend upon the extent of overlap between grazing and cutthroat trout populations and whether those populations face concurrent threats that have already reduced their abundance and resilience and contributed to environmental variability. Overlap between livestock grazing and the occurrence of native fishes can be extensive. Salvo (2009) assessed the distribution of six species or subspecies of inland *Oncorhynchus* (including westslope cutthroat trout) in the western United States relative to permitted grazing allotments and estimated that 17–76% of the current stream range intersects or is contained within allotments. In southwestern Montana the overlap can be even greater, as 79% of the stream miles occupied by westslope cutthroat trout within the Beaverhead-Deerlodge Forest boundary are in grazing allotments (J. A. Brammer, *unpublished data*). The extent of concurrent threats and the loss of resilience over the range of westslope cutthroat trout have not been quantified, but change has been widespread. Westslope cutthroat trout populations in southwestern Montana face multiple stressors, including habitat degradation and fragmentation (Shepard et al. 1997, 2005), and reduced recruitment and survival associated with nonnative trout invasions (Dunham et al. 2002, Shepard et al. 2002, Peterson et al. 2004). Most westslope cutthroat trout east of the Continental Divide in Montana are in remnant, isolated populations (Shepard et al. 2005) in which the loss of migratory life histories has probably constrained individual growth, fecundity, and, consequently, resilience (e.g., Fausch et al. 2009). Trout populations exposed to cattle trampling also occupy habitats that may be degraded from grazing effects, which can also constrain reproduction and recruitment (e.g., Platts 1991, Armour et al. 1994). Across western North America, changing climate is anticipated to bring more extreme events such as droughts, floods, and large fires (e.g., McKenzie et al. 2004, Hamlet and Lettenmaier 2007) and has already been associated with increased interannual variability in stream flows and earlier spring runoff in snow-dominated watersheds (Luce and Holden 2009). All of these habitat and biotic limitations and interactions will operate concurrently in many cutthroat trout populations (Shepard 2004) and would be likely to reduce resilience and increase the vulnerability to additional mortality at any life history stage.

Model limitations and caveats

The models we built to represent trampling effects on egg-to-fry mortality and population growth are simplified representations of ecological processes. Input variables are generalizations useful for contrasting trampling rate and timing in different contexts, and model predictions may be more or less conservative, depending upon the validity of key assumptions. Although the results may prove useful for evaluating riparian grazing by cattle, they cannot be interpreted literally.

We estimated a trampling effect based on laboratory experiments that tested effects of angler wading (Roberts and White 1992) because there were no corresponding data for cattle. We also assumed that trampling rates observed in a field study using artificial redds are equivalent to trampling of embryos in actual redds and that the trampling rates apply to the entire population. Trampling by cattle could result in greater mortality of embryos and preemergent fry than caused by human wading (Roberts and White 1992) because of their larger body mass and force applied during trampling, so we may have underestimated this effect. Moreover, we ignored trampling by native ungulates, so overall trampling effects were underestimated. Our models are not spatial, and we assume the location of redds and trampling is random. Redds are not randomly distributed in wild populations of resident westslope cutthroat trout (e.g., Magee et al. 1996). Consequently, actual trampling of redds may be less or more, depending upon spatial correlation between spawning site location, or the landscape and channel characteristics that influence site selection, and cattle behavior. The population model also assumed that any trampling effects occurred each year, so our growth rate and persistence will be underestimated if trampling occurs less frequently.

By design we enforced compensation by conceiving different population scenarios in which egg-to-fry mortality varied (from low to high) and mortality at other life stages was adjusted to achieve a desired population growth rate in the absence of trampling. We did not, however, directly model compensation that might result from trampling, and this was a key simplification for the modeling exercise. If these compensatory effects were strong, then the models would overestimate the population-level effect of trampling because additional mortality from trampling would be offset by lower mortality at different life stages of the population. Density dependence and compensation are generally assumed to regulate many salmonid populations, but demonstrating their existence and the form of the density dependence or stock–recruitment relationship is difficult (Zabel and Levin 2002, Milner et al. 2003). This problem may be mitigated for low-density populations that likely exist below the abundance at which density-dependent processes have a strong influence. Density-dependent effects on mortality are often ignored when population models are applied to salmonid populations at low abundance (e.g., Wilson 2003, McHugh et al. 2004, but see Zabel et al. 2006). Low abundance may be typical of resident cutthroat trout populations constrained by other physical habitat and biotic stressors, so the simplifying assumption of no density dependence seems reasonable for the initial investigation of trampling effects.

Results are model-specific, and population-level outcomes are sensitive to model structure, model parameterization, and analytical purpose. Egg-to-fry mortality is difficult to estimate in wild salmonid populations, and literature values or those assumed in cutthroat trout population models range widely (0.50–0.95; see Magee et al. 1996, Shepard et al. 1997, Stapp and Hayward 2002). By design, the overall effect on trampling in the matrix model directly depended on the relative sensitivity of population growth rate to egg-to-fry mortality, as this was the only demographic rate permitted to vary. Other cutthroat trout population models developed to assess effects of nonnative species (Stapp and Hayward 2002, Peterson et al. 2008*a*), efficacy of supplementation strategies (Hilderbrand 2002), or environmental variation and carrying capacity (Hilderbrand 2003) have assumed λ is more sensitive to changes in juvenile and subadult mortality than egg-to-fry mortality, fewer scenarios for egg-to-fry mortality, and different spawning frequencies. Models presented in Hilderbrand (2003) and Peterson et al. (2008*a*) couple low egg-to-fry mortality ($\leq$0.60) with moderate-to-high λ (1.06 and 1.10, respectively) and assume females spawn each year. With mean summer temperature of 9.6°C, trampling rates of $>$135% to 500% would be needed to increase egg-to-fry mortality enough (to 0.688 and 0.695) to cause deterministic population decline under those models. This result does not imply that trampling is less important than we present based on our models. Rather, we feel it emphasizes the future importance of obtaining robust demographic information to validate these types of models.

Our egg-to-fry and matrix population models were deterministic. However, we addressed parameter uncertainty by considering a range of values (e.g., in egg-to-fry mortality, trampling rates, etc.), and estimates of persistence using the diffusion approximation method considered environmental variation in population growth. In general, models that incorporate variation in individual vital rates (stochasticity) will be more pessimistic than deterministic models in terms of persistence (Morris and Doak 2002) or long-term population size, especially if density dependence is also considered (e.g., Van Kirk and Hill 2007).

Management implications

Despite their limitations, the models can provide guidance for addressing cattle management where trampling of native cutthroat trout redds may be a concern. A cautionary approach to cattle grazing in riparian zones could be warranted, especially for populations that are already compromised by other stressors and particularly during mid-summer when developing embryos are most sensitive to disturbance.

An increase in egg-to-fry mortality is expected from any amount of redd trampling, so the most conservative approach would be to limit cattle activity in riparian zones and stream channels when trout embryos are most vulnerable, in this case mid-July through mid-August. The egg-to-fry model should be validated and could be extended in its applicability and detail. Stream temperature and observed dates of cutthroat trout spawning and emergence could be used to validate predictions for temporal vulnerability to trampling. Validating model-based mortality estimates for a given level of trampling would be much more difficult to determine in wild populations. The model's approach could be extended to more explicitly consider uncertainty in spawning dates, environmental variability, spatial variation (e.g., Vander Zanden et al. 2007), alternative or complementary metrics of population response (e.g., Van Kirk and Hill 2007), or to address conservation of other native fishes potentially affected by grazing.

Our analyses indicate that the underlying model assumptions and estimates of stage-specific mortality in cutthroat trout are two sources of uncertainty that could justify further investigation. Reductions in trout density have been associated with livestock grazing in riparian zones (e.g., Platts 1991, Belksy et al. 1999), but the specific role redd trampling may play in these declines has not been considered. Laboratory and field investigation may help determine whether mortality between artificial and actual redds differs and assess how grazing effects may vary between wild and native ungulates (e.g., Albon et al. 2007). Empirical data and additional modeling could be focused on the issue of population regulation and compensation in low-abundance trout populations (Milner et al. 2003), because land and water management activities are often adjusted to promote conservation of sensitive fish stocks (Zabel and Levin 2002).

Trampling by cattle has long been recognized as a potential source of mortality for native species rangeland habitats including plants, reptiles, and ground-nesting birds (Guthery and Bingham 1996). Similar impacts to species that inhabit ecotones between terrestrial and aquatic habitats, such as insects (Bates et al. 2007) or amphibians (Adams et al. 2009), or strictly aquatic species such as fishes (Gregory and Gamett 2009), have only recently received more focused consideration. Cattle grazing is one of the most pervasive uses of semiarid landscapes in western North America (Belsky et al. 1999), and the ecological importance of riparian and aquatic habitats within those landscapes is widely recognized (Fleischner 1994). Evaluation of grazing policies on some federal lands may be needed to ensure species conservation and land use concerns are equitably balanced.

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APPENDIX A

Derivation of finite mortality for cutthroat trout embryos resulting from redd trampling by cattle (*Ecological Archives* A020-033-A1).

APPENDIX B

Matrix population model for stream-resident cutthroat trout in southwestern Montana, USA, used to estimate effects of redd trampling by cattle (*Ecological Archives* A020-033-A2).