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ARTICLE

Effects of Air Exposure During Simulated Catch-and-Release Angling on Survival and Fitness of Yellowstone Cutthroat Trout

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Abstract

Concerns have been raised regarding the practice of exposing fish to air during catch-and-release (C&R) angling. The purpose of this study was to evaluate the effects of air exposure on short- and long-term survival and progeny production of Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri*. Prespawn adults were sampled at a weir during upstream migration in 2016 and 2017, exposed to a simulated angling event of 102 s, and then exposed to air for a randomly selected duration of 0, 30, or 60 s. An additional control group was added during 2017 in which fish were not exposed to simulated angling or air. In total, 1,519 fish were sampled in 2016, and 744 fish were sampled in 2017. Additionally, age-0 fish (2016: *n* = 2,924; 2017: *n* = 1,492) were collected to evaluate the effects of air exposure on the production of progeny. No effect of angling itself or of angling and air exposure was observed on short-term (≤60 d posttreatment) or long-term (>1 year posttreatment) survival of adults, with one exception. During 2016, fish that had been air exposed for 60 s had a statistically higher short-term survival rate than fish that received no air exposure. Air exposure had no effect on the proportion of fish that successfully spawned. Regression analysis revealed that neither angling nor air exposure affected progeny production. Considering that much of the literature, as well as this study, reports little to no influence of air exposure on salmonid mortality or reproductive success, it seems highly unlikely that air exposure of less than 60 s during C&R angling would have negative population-level effects.

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Fishing regulations are used by natural resource agencies to accomplish an array of management objectives, including a focus on improving the quality of a fishery or maintaining the viability of a population (Isermann and Paukert 2010). In some cases, managers use regulations to manipulate fish assemblages (Schneider and Lockwood 2002) and to remove undesirable species (Goeman et al. 1993). In other cases, managers implement regulations for social purposes, perhaps misunderstanding their biological merits (Schill and Scarpella 1997). The most commonly implemented management actions are seasonal closures, bag and length limits, gear restrictions, and catch-and-release (C&R) regulations (Isermann and Paukert 2010).

The term "catch and release" has multiple connotations, at times referring to fisheries where anglers are required to release all of their catch and in other cases referring to fisheries where anglers simply choose to release some or most of their catch (Lamansky and Meyer 2016). We use the term "catch and release" to denote both types of fisheries in this paper. Catch-and-release regulations were first envisioned and implemented in salmonid fisheries (Thompson 1958) but have become increasingly popular in other recreational fisheries (Isermann and Paukert 2010). Natural resource agencies implement C&R regulations for a variety of reasons, but the primary purpose is to reduce exploitation and increase density, size structure, or both. A number of studies has shown the benefits of C&R regulations on fish populations that experience high angler use. For example, Kelly Creek, Idaho, displayed improved catch rates after C&R regulations were implemented for Westslope Cutthroat Trout *Oncorhynchus clarkii lewisi* (Johnson and Bjornn 1978). When regulations allowed for angler harvest in Kelly Creek, catch rates were 1 fish/angler-hour. After 5 years of C&R regulations, catch rates doubled to 2 fish/angler-hour.

Despite the success and widespread use of C&R regulations, some concerns have been raised regarding the practice. Exposing fish to air during release is one of the most high-profile of these concerns (Cook et al. 2015). Air exposure is associated with a number of direct effects in caught-and-released fish. Direct effects are those in which air exposure directly influences mortality or generates sublethal effects (e.g., on reproductive success, the ability to cope with thermal stress, or swimming performance). For example, air exposure is believed to temporarily suppress gas transfer across the gills, which can lead to hypoxia and increased levels of carbon dioxide in the bloodstream (Ferguson and Tufts 1992). Numerous studies have attempted to address the question of how long a fish must be exposed to air before it experiences sublethal effects or mortality. However, many studies have reported little to no effect on fish survival or reproductive success after air exposures of 2 min or longer (e.g., Schisler and Bergersen 1996; Schreer et al. 2005; Suski et al. 2007; Gale et al. 2011; Raby et al. 2013).

In addition to direct mortality, a small number of studies ($n = 2$) has evaluated the effects of air exposure on reproductive success, with vastly different conclusions (Raby et al. 2013; Richard et al. 2013). Atlantic Salmon *Salmo salar* in the Escoumins River, Quebec, were reported to experience decreased reproductive success when exposed to air (Richard et al. 2013). Fish exposed to air for more than 10 s reportedly had two to three times lower reproductive success compared to fish exposed to air for less than 10 s. Proponents of limiting air exposure often cite the decline in reproductive success observed by Richard et al. (2013) as evidence for limiting air exposure (e.g., Cook et al. 2015). Conversely, it was reported that upon reaching their spawning grounds in Weaver Creek, British Columbia, Chum Salmon *O. keta* and Pink Salmon *O. gorbuscha* were resilient to any effects of C&R angling (Raby et al. 2013). In fact, no decline in spawning success was reported after simulated capture and 1 min of air exposure.

Given the variable and often contradictory results reported in the air exposure literature, further study of air exposure's effects on sport fishes is warranted before regulations limiting the amount of time that anglers can expose fish to air during C&R angling are seriously contemplated or implemented (e.g., WDFW 2016). Furthermore, the artificial nature of many past air exposure studies (e.g., use of hatchery fish, tail grabbing, and lack of actual angling) calls for additional studies on wild fish under conditions that are transferable to real-world C&R events (Roth et al. 2018b). The overall goal of this study was to better understand the influence and relevance of air exposure on the survival and reproductive success of spawning wild Yellowstone Cutthroat Trout *O. clarkii bouvieri* under conditions similar to those the fish would experience during actual C&R angling. The Yellowstone Cutthroat Trout is an ideal species for evaluating the effects of air exposure because salmonids are among the most sensitive taxa with regard to hypoxia (Doudoroff and Shumway 1970) and they support important recreational fisheries throughout the Intermountain West (Quist and Hubert 2004). The specific objectives of this study were to evaluate the effects of air exposure during an upstream spawning migration on (1) the short- and long-term survival of postspawn adult Yellowstone Cutthroat Trout and (2) the reproductive success of Yellowstone Cutthroat Trout.

STUDY AREA

This study was conducted on Burns Creek, Idaho (Figure 1), in the South Fork Snake River (SFSR) drainage from May to October 2016 and from May to September

2017. Burns Creek is a third-order tributary of the SFSR (Moore and Schill 1984). Discharge in Burns Creek typically varies from 0.1 to 9.0 m^3/s, and channel gradient is 3–6%. A large portion of the Yellowstone Cutthroat Trout population in the SFSR displays a fluvial life history, with fish moving from the main-stem SFSR into Burns Creek and other tributaries to spawn (Thurow et al. 1988). Yellowstone Cutthroat Trout in the SFSR mature around age 4; spawning begins in late May and continues through early July. Approximately 2 weeks after spawning, adults migrate from Burns Creek back to the main-stem SFSR. Fry typically emerge from mid-July through September and out-migrate to the SFSR as age-0 fish (Moore and Schill 1984; Thurow et al. 1988).

METHODS

Field sampling.— Adult Yellowstone Cutthroat Trout were collected at an existing Idaho Department of Fish and Game (IDFG) velocity barrier weir on Burns Creek (located 0.9 km upstream of the creek mouth) during May–July 2016 and May–June 2017 (Figure 1). Fish enter a fish ladder to navigate the weir and continue upstream. At the end of the ladder is a fish trap, where fish were held for sampling. Fish were removed from the trap with a dip net, placed into a bucket, and then transported to holding tanks to await processing, all the while remaining underwater. While the gills remained underwater, a 12-mm, full-duplex PIT tag was inserted into the peritoneal cavity of each fish (Prentice et al. 1990). Returning fish that already contained a PIT tag from a prior spawning year were scanned to record the tag number, and a needle was inserted into the peritoneal cavity to mimic a PIT tag injection. All newly PIT-tagged fish had their adipose fin removed as a secondary mark, and the sampled fin was retained for individual genetic identification. For fish lacking an adipose fin, tissue samples were taken from the upper caudal fin. Tissue samples were stored on Whatman 3MM chromatography paper (Thermo Fisher Scientific, Inc., Pittsburgh, Pennsylvania) for genetic analysis at the IDFG Eagle Fish Genetics Lab. The phenotypic sex of each fish was identified in the field and confirmed using genetic analysis to produce accurate sex assignments (i.e., 99% accuracy in field-based assignments; Schill et al. 2016). While remaining underwater, each fish had a 1/0 barbed circle hook manually inserted through the middle of the lower jaw and was randomly assigned a treatment of 0 s (control), 30 s, or 60 s of air exposure. An additional treatment group was added during 2017 wherein fish were neither played nor exposed to air (NF group). The fish was quickly maneuvered into a submerged, 102.0-mm acrylic tube, measured for TL (mm), and carried upstream of the weir, all while remaining underwater. Angling gear was attached to the circle hook in the fish's lower jaw, and the fish was returned to the river while remaining underwater and was played to simulate angling. Each fish was played for 102 s, corresponding to the average fight time for spawning-sized Yellowstone Cutthroat Trout in a C&R fishery on the Yellowstone River (Schill et al. 1986). However, it is worth noting that average fight times on the SFSR were subsequently reported to be much lower (i.e., 40 s; Roth et al. 2018a). After being played, the fish was netted using a rubber-meshed net, unhooked, treated with its prescribed amount of air exposure, and returned to the river to move upstream and spawn. Water temperatures in Burns Creek were continuously monitored during the sampling period in both years of the study. Water temperatures in the creek averaged 11.8°C (SE = 0.4) and varied from 5.7°C to 16.8°C during 2016. In 2017, water temperatures averaged 10.4°C (SE = 0.3) and varied from 6.1°C to 13.8°C.

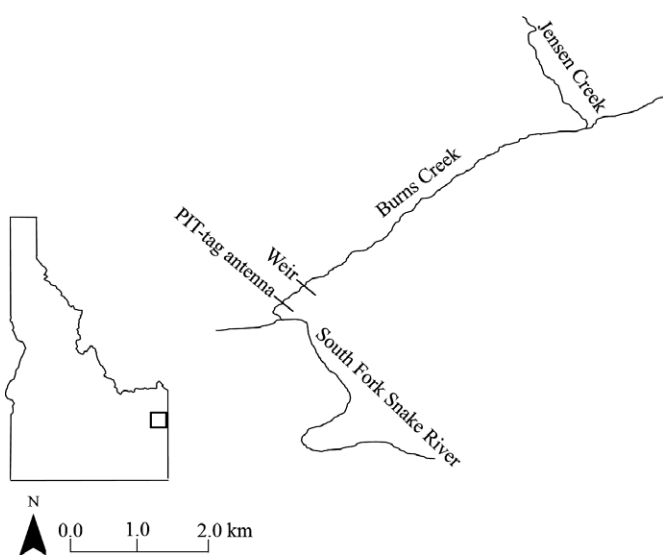

FIGURE 1. Map of Burns Creek, Idaho, from its confluence with the South Fork Snake River to its confluence with Jensen Creek.

Two postrelease survival estimates for these fish were obtained. An estimate of short-term relative survival by treatment group was calculated using two fixed PIT antennas located 0.5 km downstream of the weir to detect postspawn adult fish as they out-migrated back to the SFSR. Specifically, the proportion of postspawn adult Yellowstone Cutthroat Trout that moved past the PIT antenna within 60 d of their tagging date was used to characterize short-term survival similar to Rapp et al. (2014). It is important to note that relative survival does not reflect actual survival; rather, it is the difference in proportions of fish from each treatment group that were detected at the antenna. Estimates of short-term relative survival could differ from actual survival for a number of reasons, such as tag loss or antenna error. Adults detected by the

PIT antenna were assigned back to their air exposure treatment to estimate survival. Additionally, an estimate of relative survival at 1 year (long-term survival) was calculated by matching the genotypes of fish out-migrating past the PIT-tag detector in 2016 with those of fish returning to the weir in 2017. Again, long-term survival likely differs from actual survival for various reasons, including skipped spawning, lack of fidelity to Burns Creek, or spawning downstream of the weir. However, estimates of both short- and long-term relative survival will hereafter be referred to as estimates of survival following Schill (1996) and Roth et al. (2018b).

Once adult trapping had concluded, we began collection of out-migrating age-0 Yellowstone Cutthroat Trout to evaluate the effect of air exposure on the subsequent production of progeny for individual adults in each treatment group. Fry collection was conducted using two trapping methods and electrofishing. Fry were collected by using (1) a modified picket weir located approximately 25 m downstream of the IDFG velocity barrier weir and (2) two Kray–Meekin traps placed in the thalweg downstream of the picket weir. Trapping took place continuously during July–October in both 2016 and 2017. During 2016, only one Kray-Meekin trap and the modified picket weir were used to trap fry. In 2017, fry were trapped using two Kray–Meekin traps. A random subsample of fish captured in the traps each day was used for the genetic analysis (see below). To supplement these samples, single-pass backpack electrofishing was conducted to collect fry for genetic analysis during September and October 2016 and September 2017. Electrofishing took place over two 2-d periods in 2016 and a single 2-d period in 2017. In both 2016 and 2017, fry sampled via backpack electrofishing were placed into buckets. Caudal fin tissue was removed from a random subsample of fry from each bucket. Burns Creek was sampled from the existing IDFG velocity barrier weir to a location 4 km upstream, an area where the majority of fluvial Yellowstone Cutthroat Trout spawn (B.H., unpublished information). Tissue samples were analyzed at the IDFG Eagle Fish Genetics Lab.

Genetic analysis.— Our general approach was to use parentage-based tagging to identify individual fry as having been produced by specific individuals that were sampled as prespawn adults (Steele et al. 2013) and subsequently to compare levels of progeny production for fish that had experienced one of the different air exposure treatment regimes (Richard et al. 2013). We extracted DNA from all samples by using the nexttec Genomic DNA Isolation Kit (XpressBio, Thurmont, Maryland). All samples were screened with a panel of 134 single-nucleotide polymorphic (SNP) loci. One of these SNP loci (*2017SDYCUT*) differentiates sex in Yellowstone Cutthroat Trout. This marker was redesigned from the Y-chromosome-specific assay (*OmyY1*) developed by Brunelli et al. (2008). The primer sequences for *2017SDYCUT* were as follows: 5′-GTGGAGTACTG CGAAGAGGA-3′ (forward) and 5′-AAAACCACTCCAC CCTCCAT-3′ (reverse). Prior to use, we confirmed the accuracy of this marker by screening known-sex samples of broodstock from the IDFG Henrys Lake Hatchery (100 males and 100 females). All genetic calls matched phenotypic sexing. Genetic sex was not included in parentage analyses, but all parent assignments were checked to confirm that they were between a male and a female.

The remaining 133 SNP loci in the panel were used for parentage analyses. These SNP loci were identified and developed from restriction site-associated DNA sequencing performed in the IDFG Eagle Fish Genetics Lab (M.R.C., unpublished information). Primer sequences for these SNP loci are available from the authors upon request. Genotyping of the SNP panel followed genotyping-in-thousands sequencing protocols developed by Campbell et al. (2015).

Parentage assignments were performed using the program SNPPIT (Anderson 2010). We required an 80% complete genotype (minimum of 106 loci) for a sample to be included in the analyses, and we used an estimated SNP genotyping error rate of 1% or a per-allele rate of 0.5%. The program uses a maximum likelihood algorithm for parentage assignments (Anderson 2010). In SNPPIT, a successful assignment is classified as "C_Se_Se," which stands for a trio relationship of "Candidate Offspring_ True Parent_True Parent." The Se refers to "Self" and is used to distinguish a relationship involving a "Si" (sibling of a true parent) from those involving "Se" (self) and "U" (unrelated). The confidence of this trio relationship can be evaluated using the logarithm of odds (LOD) score reported in SNPPIT. The LOD score is the natural logarithm of the likelihood of the parental trio hypothesis divided by the likelihood of the nonparental hypothesis for a trio. We calculated the range of LOD scores observed for known parent-pair trios to set threshold criteria for assignments. We also estimated type I and type II error rates of our SNP marker panel. Type I error is assigning an untrue parent pair, and type II error is failing to assign a true parent pair (Araki and Blouin 2005). To accomplish this, we simulated offspring genotypes from adults passed above the weir in 2017 (n = 744). For type II error, we simulated 1,000 offspring and then included all adults from 2017 and all juvenile fish collected in 2016 (n = 2,924) as potential parents in our candidate parent file. This testing identified one incorrect trio combination (one incorrect parent assigned), for an error rate of 1/1,000 = 0.001. For type I error testing, we performed two tests. In the first test, we used the same 1,000 simulated offspring as before, but we removed all known female parents. We still included all juvenile fish collected in 2016. Of the 1,000 simulated offspring, 18 were assigned with a C_Se_Se assignment in SNPPIT (error rate = 0.018).

However, only one fish was assigned with an LOD value greater than 18 (error rate = 0.001). Based on these results, we used this value as a threshold for parentage assignments in the study data set. In the second type I error test, we used the same data sets as used in the first test except that we removed all known parents. Under this test, no simulated offspring was assigned to a parent pair with an LOD greater than 18 (error rate = 0.000).

Data analysis.— The effects of air exposure on the short-term survival of adult Yellowstone Cutthroat Trout were evaluated by calculating the proportion of fish from each treatment group that were detected moving downstream past the PIT antenna located in lower Burns Creek. The proportions provided an estimate of survival. Ninety-five percent confidence intervals (CIs) for the proportions were calculated using the standard formula for proportions (Zar 1996),

$$p \pm 1.96\sqrt{\frac{p(1-p)}{n}},$$

where p is the sample proportion and n is the sample size. The proportions of recaptured fish were compared between treatment groups by calculating 95% CIs around the differences between proportions via the formula of Fleiss (1981), with the lower limit given by

$$(p_2 - p_1) - c_{\alpha/2}\sqrt{\frac{p_1 q_1}{n_1} + \frac{p_2 q_2}{n_2}} - \frac{1}{2}\left(\frac{1}{n_1} + \frac{1}{n_2}\right)$$

and the upper limit given by

$$(p_2 - p_1) + c_{\alpha/2}\sqrt{\frac{p_1 q_1}{n_1} + \frac{p_2 q_2}{n_2}} + \frac{1}{2}\left(\frac{1}{n_1} + \frac{1}{n_2}\right),$$

where n_1 and n_2 are sample sizes; p_1 and p_2 are the two recapture proportions; $q_1 = 1 - p_1$; $q_2 = 1 - p_2$; and $c_{\alpha/2}$ is 1.96. Estimates of survival were considered significantly different between groups when 95% CIs around the differences did not contain zero (Fleiss 1981; Johnson 1999; Schill et al. 2016). Such an approach is a direct statistical test, with the added benefit of clearly identifying both an effect size and the associated precision (Johnson 1999). The same method was used to evaluate long-term survival between 2016 and 2017.

The second objective of the study was to evaluate the effects of air exposure on the reproductive success of spawning Yellowstone Cutthroat Trout. The air exposure effect on reproductive success was first examined by calculating the proportion of fish that produced at least one offspring in each treatment group. Proportions were then compared by calculating confidence bounds around the difference between proportions (Fleiss 1981; Johnson 1999).

Generalized linear models with a negative binomial distribution (Richard et al. 2013) were also used to evaluate the effects of air exposure on reproductive success in more detail. Models were analyzed using the MASS package (Venables and Ripley 2002) in R (R Core Team 2017). For the purpose of modeling, data were pooled between years because (1) handling protocols were the same between years (with the exception of fish in the NF treatment group) and (2) preliminary analysis indicated consistent patterns among years. Fish in the NF treatment group were removed from the pooled data analysis because 2016 lacked an NF treatment group and preliminary analysis of the 2017 data indicated no difference between NF and the other treatments (see below). Two sets of candidate models were developed: one set using only data collected from adult male Yellowstone Cutthroat Trout (male-only models), and a second set using only data collected from adult female Yellowstone Cutthroat Trout (female-only models). Eight candidate models were developed for both male- and female-only models. A priori models included the following: (1) a model including only fish TL and year; (2) a model including air exposure treatment and year; (3) a model including air exposure treatment, fish TL, and year; and (4) a model including air exposure treatment, fish TL, the fish TL × treatment interaction, and year. All four models were repeated without year as a covariate. Models were compared using Akaike's information criterion corrected for small sample size (AIC_c), and the top model was the one with the lowest AIC_c value (Burnham and Anderson 2002). Models that had an AIC_c score within 2.0 units of the best model's score were also considered as belonging to the set of top models. Models were assessed for overdispersion using the dispersion parameter ($\hat{c}$) and were considered overdispersed when $\hat{c}$ was greater than 1.0 (Burnham and Anderson 2002). The dispersion parameter was calculated by dividing Pearson's residual deviance by the residual degrees of freedom. Overdispersed models had an additional parameter added to adjust for the estimation of dispersion. Model fit was assessed using McFadden's pseudo-R^2 (McFadden 1974). McFadden's pseudo-R^2 values of 0.20–0.40 are considered to indicate excellent model fit (Hosmer and Lemeshow 1989). Additionally, the NF treatment was evaluated by comparing that treatment to the other three treatments using only the 2017 data. The top male-only and female-only models were used for this analysis without year as a covariate. Based on this analysis, no difference was observed between the NF treatment and the other treatment groups.

RESULTS

In total, 1,519 upstream-migrating adult Yellowstone Cutthroat Trout were sampled in 2016 and assigned to a

treatment group (0 s: n = 485; 30 s: n = 494; 60 s: n = 534). In 2017, 744 fish were sampled (NF: n = 176; 0 s: n = 167; 30 s: n = 206; 60 s: n = 195). Length distributions were virtually identical among treatment groups by sex in 2016 (Figure 2) and 2017 (Figure 3). Two-hundred-twelve adults were detected as out-migrating (0 s: n = 55; 30 s: n = 72; 60 s: n = 85) in 2016, and 314 adults (NF: n = 64; 0 s: n = 71; 30 s: n = 92; 60 s: n = 87) were detected as out-migrating in 2017. Short-term survival was similar among treatments, and the proportion of detected fish varied from 0.11 to 0.16 among treatment groups (0 s: 0.11; 30 s: 0.15; 60 s: 0.16) in 2016 and from 0.35 to 0.45 (NF: 0.35; 0 s: 0.41; 30 s: 0.44; 60 s: 0.45) in 2017. No statistical difference in short-term survival was observed in 2016 between fish treated with 0 and 30 s of air exposure or between fish treated with 30 and 60 s of air exposure (Figure 4). However, fish that were exposed to air for 60 s had a statistically higher estimated short-term survival rate than fish that were not exposed to air. No statistical difference in short-term survival due to air exposure was observed among all three treatments in which the fish were played to simulate angling in 2017

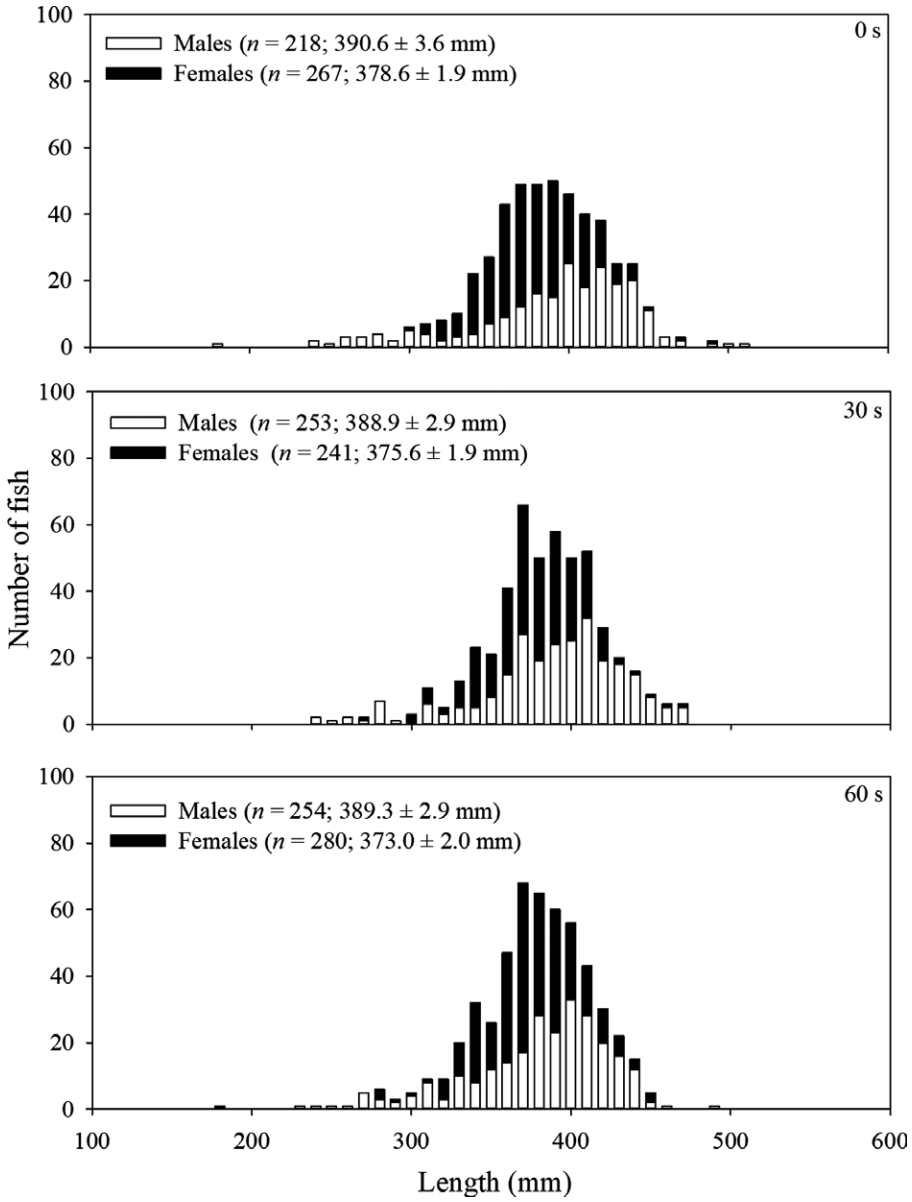

FIGURE 2. Length-frequency distributions of male and female Yellowstone Cutthroat Trout that were sampled at a velocity barrier weir on Burns Creek, Idaho (May–July 2016); played for 102 s; and exposed to air for 0, 30, or 60 s. Mean TLs (±SE) for males and females of each treatment group are presented at the top of each panel.

(Figure 4). Additionally, no statistical difference was observed in survival due to angling based on the NF treatment group. The proportion of adults sampled in 2016 and then resampled in 2017 varied from 0.06 to 0.08 (0 s: 0.07; 30 s: 0.08; 60 s: 0.06). No statistical differences in long-term survival were observed among treatment groups (Figure 5).

In 2016, 2,924 fry were sampled (electrofishing: n = 2,175; Kray–Meekin trap: n = 583; picket weir: n = 166); in 2017, 1,492 fry were sampled (electrofishing: n = 1,100; Kray–Meekin traps: n = 392). All 2,924 fry sampled in 2016 were successfully genotyped. Of those fry, 2,310 assigned back to two parents that were handled at the weir as prespawn adults during the study. In 2017, 1,490 of the 1,492 sampled fry were successfully genotyped, and 650 were assigned back to two parents that were handled as part of the study.

Air exposure treatment had no statistical effect on the number of male and female fish that successfully spawned and produced one or more progeny (Figure 6). The proportion of males that successfully spawned varied from 0.48 to 0.55 (0 s: 0.48; 30 s: 0.55; 60 s: 0.51) in 2016 and

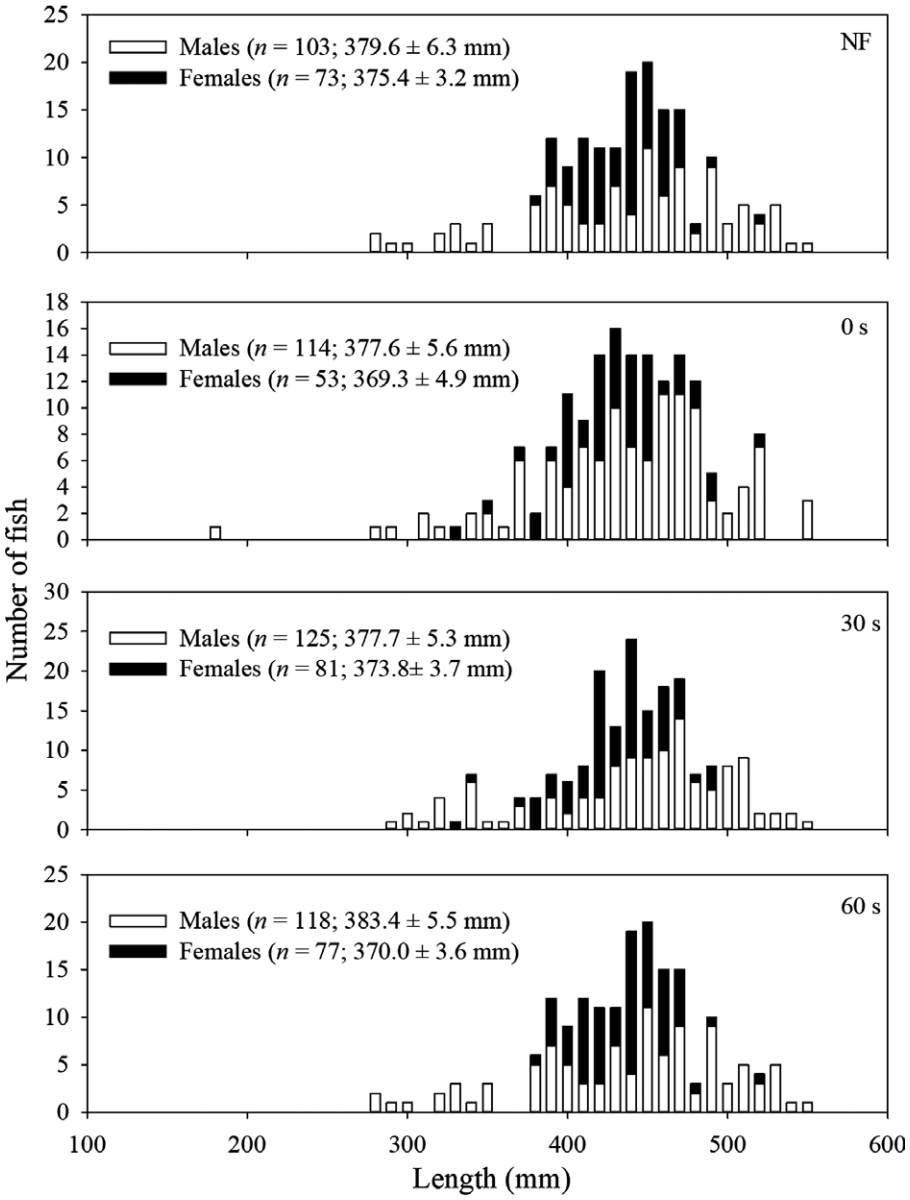

FIGURE 3. Length-frequency distributions of male and female Yellowstone Cutthroat Trout that were sampled at a velocity barrier weir on Burns Creek, Idaho (May–June 2017); played for 102 s; and exposed to air for 0, 30, or 60 s. In addition to the three air exposure treatments, an NF treatment (in which fish were neither played nor air exposed) was included during 2017. Mean TLs (±SE) for males and females of each treatment group are presented at the top of each panel.

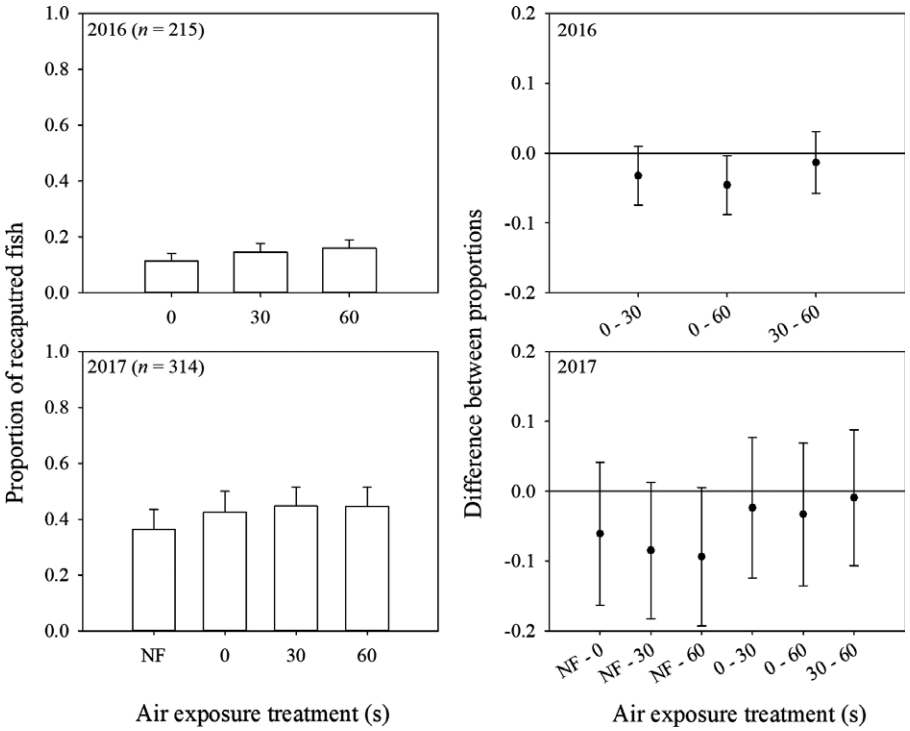

FIGURE 4. Proportions (+SE) of adult Yellowstone Cutthroat Trout (left panels) that were detected as out-migrating from Burns Creek, Idaho, within 60 d of an air exposure treatment (May–August 2016; or May–August 2017). Differences between the proportions (±95% confidence interval [CI]; right panels) were calculated as the proportion for the shorter-duration air exposure group minus the proportion for the longer-duration air exposure group. Values below the zero line indicate that fish in the treatment group with less air exposure had lower survival than the fish in the treatment group with a longer air exposure duration. The NF treatment (in which fish were neither played nor air exposed) was added in 2017. Differences were considered statistically significant if the 95% CI did not overlap the zero line.

from 0.28 to 0.33 (NF: 0.28; 0 s: 0.32; 30 s: 0.33; 60 s: 0.31) in 2017. Results were similar for females, with the proportion that successfully spawned varying from 0.59 to 0.66 (0 s: 0.66; 30 s: 0.59; 60 s: 0.60) in 2016. The proportion of females that successfully spawned in 2017 varied from 0.44 to 0.48 (NF: 0.48; 0 s: 0.45; 30 s: 0.44; 60 s: 0.45).

The top male-only model predicting the number of progeny produced contained air exposure treatment, fish TL, and year as predictors (Table 1). However, model fit was poor (i.e., McFadden's pseudo-R^2 = 0.06), and a graphical depiction of this model showed a lack of an observable air exposure effect (Figure 7). For example, the regression lines for the 0-s and 60-s treatments virtually obscured each other. Based on the top model, the number of offspring produced by male Yellowstone Cutthroat Trout increased with TL. Results of regression analysis for the female-only models were similar to those for males, with the top model containing air exposure treatment, fish TL, and year (Table 1). As with the male-only model, model fit was poor (McFadden's pseudo-R^2 = 0.02). Again, the graphical representation demonstrated a lack of observable air exposure effects, and the number of offspring produced increased with female TL (Figure 8). Results were similar for the models evaluating the effects of the NF treatment using only the 2017 data (data not presented). In both male- and female-only models, production of progeny increased with TL; however, model fit was poor (i.e., male-only model: McFadden's pseudo-R^2 = 0.04; female-only model: McFadden's pseudo-R^2 = 0.01).

DISCUSSION

Numerous studies have been conducted to evaluate the effects of removing fish from the water during C&R angling, particularly the effects of air exposure on mortality (e.g., Ferguson and Tufts 1992; Gingerich et al. 2007; Suski et al. 2007; Thompson et al. 2008; Rapp et al. 2014; Graves et al. 2016; Louison et al. 2017; Gagne et al. 2017; Roth et al. 2018b; Twardek et al. 2018). Unfortunately, much of the existing air exposure literature suffers from limitations that make it difficult to apply the results to wild fish populations. For instance, the use of holding tanks and hatchery fish (Ferguson and Tufts 1992; Suski et al. 2007) is unlikely to generate results that are

transferable to wild fish in natural systems. Furthermore, several of these studies are limited by unrealistic simulations of angling. Ferguson and Tufts (1992) and Suski et al. (2007) used tail grabbing to simulate angling. In addition, fish were chased for 4 min (Suski et al. 2007) or 10 min (Ferguson and Tufts 1992). Although the literature on actual fight times is sparse, the times implemented in these studies are likely unrealistically long. For instance, Schill et al. (1986) reported that the average fight time was 102 s for Yellowstone Cutthroat Trout in Yellowstone National Park, Wyoming. Recent research on salmonids in Idaho has shown that fight time averages less than 1 min (Lamansky and Meyer 2016; Roth et al. 2018a). Even trophy steelhead (anadromous Rainbow Trout *O. mykiss*) have an average fight time of about 3 min (Chiaramonte et al. 2017). Average fight times for warmwater and coolwater species (e.g., black bass *Micropterus* spp., crappies *Pomoxis* spp., and Yellow Perch *Perca flavescens*) have recently been observed to be even lower (i.e., ~20 s; Kevin Meyer, IDFG, unpublished data).

Perhaps a more apparent limitation of the existing literature is that the air exposure durations in previous research appear far greater than those experienced in actual C&R fisheries. Surprisingly, few studies have reported air exposure times in actual fisheries. In the first such study, Lamansky and Meyer (2016) reported that 96% of trout *Oncorhynchus* spp. and *Salvelinus* spp. in five fisheries across Idaho and Oregon were held out of water for 60 s or less, about 70% were exposed to air for less than 30 s, and average air exposure time was 29 s. Similar results were reported by Roth et al. (2018a) on the SFSR, Idaho: 99% of anglers exposed fish to air for less than 60 s, 84% of anglers exposed fish to air for less than 30 s, and 64% of anglers exposed fish to air for less than 20 s. Average air exposure was 19 s (Roth et al. 2018a). Recent observations for steelhead (average air exposure = 29 s; Chiaramonte et al. 2017) and warmwater and coolwater species (average air exposure = 22 s; Kevin Meyer, unpublished data) suggest nearly identical air exposure durations. In contrast, the minimum time most studies have used in air exposure treatments is 30 s (excluding control treatments; Ferguson and Tufts 1992; Schreer et al. 2005; Gingerich et al. 2007). The maximum amount of air exposure in experiments has been 30 s (Twardek et al. 2018), 2 min (Schreer et al. 2005), 3 min (Suski et al. 2007), 4 min (Louison et al. 2017), 5 min (Graves et al. 2016), 10 min (Thompson et al. 2008; Rapp et al. 2014), 16 min (Gingerich et al. 2007), and even 19 min (Brownscombe et al. 2017).

Despite the extremely long air exposure durations relative to all existing real-world air exposure times reported above, nearly all studies have reported little to no increase in mortality (Schreer et al. 2005; Suski et al. 2007; Rapp et al. 2014; Brownscombe et al. 2017; Louison et al. 2017). A single study reported mortality rates over 20% (Gingerich et al. 2007). In that effort, Bluegills *Lepomis macrochirus* were exposed to air for 0, 30, 60, 120, 240, 480, or 960 s; held in tanks at varying water temperatures (18.3, 22.8, or 27.4°C); and observed for mortality (Gingerich et al. 2007). When water temperatures were 22.8°C or lower, mortality was less than 11%, even for fish that received up to 960 s of air exposure. Mortality did not increase to over 20% until water temperature was 27.4°C and air exposure duration was 30 s or more (the highest observed mortality was 80% at 960 s). In contrast, Suski et al. (2007) exposed Bonefish *Albula vulpes* held in tanks (at Cape Eleuthera Institute, Bahamas) to air for up to 180 s and reported that a single fish suffered from

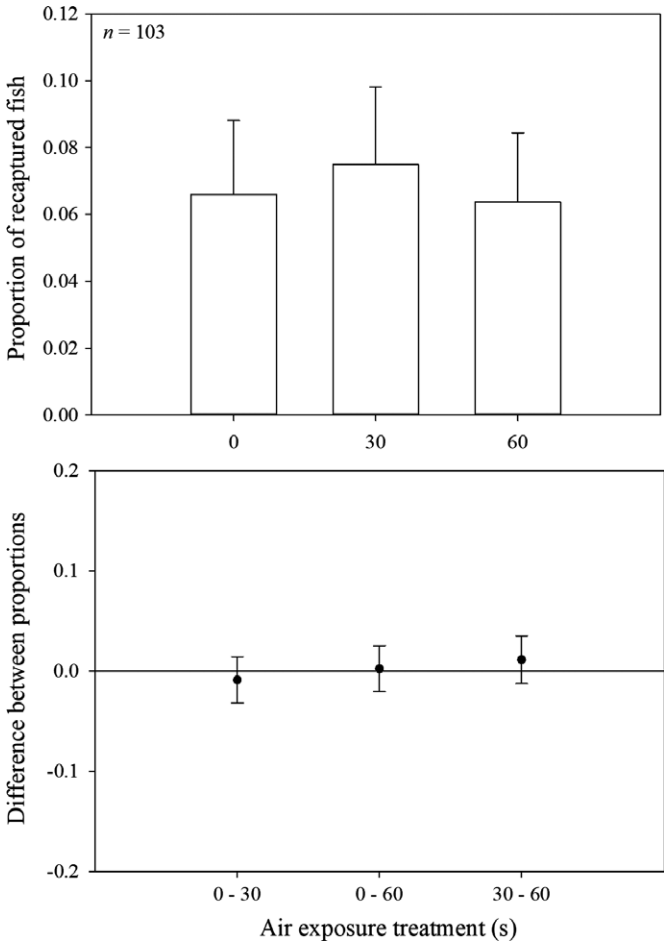

FIGURE 5. Proportions (+SE) of Yellowstone Cutthroat Trout (top panel) sampled in Burns Creek, Idaho, and given an air exposure treatment in May–July 2016 that were subsequently recaptured during May–June 2017. Differences between proportions (±95% confidence interval [CI]; bottom panel) were calculated as the proportion for the shorter-duration air exposure group minus the proportion for the longer-duration air exposure group. Values above the line indicate that survival was higher for the treatment group with less air exposure, while values below the line indicate the opposite. Differences were considered statistically significant if the 95% CI did not overlap the zero line.

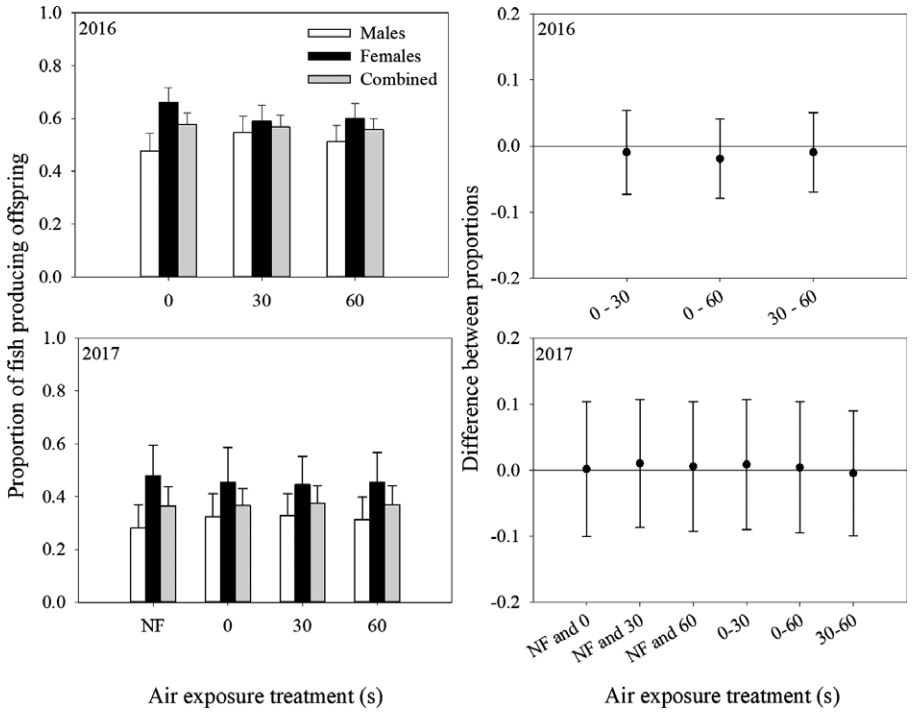

FIGURE 6. Proportions (+SE) of Yellowstone Cutthroat Trout males, females, or both sexes combined (left panels) that successfully spawned in Burns Creek, Idaho (May–October 2016; or May–September 2017), after receiving an air exposure treatment. Differences between proportions (±95% confidence interval [CI]; right panels) were calculated as the proportion for the shorter-duration air exposure group minus the proportion for the longer-duration air exposure group. Values above the line indicate that a higher proportion of fish spawned in the treatment group with less air exposure, while values below the line indicate the opposite. The NF treatment (in which fish were neither played nor air exposed) was added in 2017. Differences were considered statistically significant if the 95% CI did not overlap the zero line.

TABLE 1. Top regression models predicting the number of offspring produced by upstream-migrating adult Yellowstone Cutthroat Trout in Burns Creek, Idaho, after hooking and release using three (2016) or four (2017) different handling treatments. Models belonged to two categories: models using only data from males; and models using only data from females. Covariates include the year in which the prespawn adult was sampled, fish TL (mm), and the air exposure treatment (i.e., 0, 30, or 60 s) the fish received. The NF treatment (in which fish were neither played nor air exposed) was added in 2017. Models were evaluated using Akaike's information criterion corrected for small sample size (AIC_c), the AIC_c difference between each model and the best-performing model (ΔAIC_c), the Akaike weight (w_i), and the number of model parameters (K). McFadden's pseudo-R^2 was used to evaluate model fit.

Model	K	AIC_c	ΔAIC_c	w_i	McFadden's pseudo-R^2
		Male-only models			
Treatment + TL + Year	6	3,796.9	0.00	0.87	0.06
		Female-only models			
Treatment + TL + Year	6	4,164.3	0.00	0.41	0.02
Treatment + TL	5	4,165.0	0.62	0.30	0.02
Treatment + TL + (Treatment × TL) + Year	8	4,166.1	1.77	0.17	0.02

mortality. Other studies that exposed fish to air for 2 min (Schreer et al. 2005), 10 min (Rapp et al. 2014), or 19 min (Brownscombe et al. 2017) reported no increase in mortality due to air exposure.

We are aware of six studies that have evaluated the effects of air exposure on mortality for wild fish under conditions similar to those experienced in actual C&R fisheries (Thompson et al. 2008; Graves et al. 2016; Louison et al. 2017; Gagne et al. 2017; Roth et al. 2018b; Twardek et al. 2018). White Marlin *Kajikia albida* captured via angling off the coast of Virginia Beach, Virginia, had a mortality rate of 17% when exposed to air for 1 min (Graves et al. 2016). Mortality of White Marlin exposed to air for 5 min increased to 43%. However, the

results of Graves et al. (2016) must be interpreted cautiously. Not only were the sample sizes used in each treatment group exceptionally small (i.e., 1 min: $n = 6$; 3 min: $n = 5$; 5 min: $n = 7$), but no control treatment (i.e., fish that received no air exposure) was used during the study. Thompson et al. (2008) evaluated mortality of wild Largemouth Bass *Micropterus salmoides* in Lake Opinicon, Ontario. Fish were sampled with angling gear and were randomly assigned to and given an air exposure treatment varying from 1 to 900 s. No mortality of Largemouth Bass was observed. No increase in mortality due to air exposure (up to 120 s) was reported for Golden Dorado *Salminus brasiliensis* captured via angling in the Juramento River, Argentina (Gagne et al. 2017). Similarly, Northern Pike *Esox lucius* captured via angling in Grand Lake, Wisconsin, displayed no increase in mortality after 4 min of air exposure (Louison et al. 2017). Bull Trout *Salvelinus confluentus*, Rainbow Trout, and Yellowstone Cutthroat Trout captured via angling in Sawmill Creek, the Main Fork of the Little Lost River, and Palisades Creek, Idaho, also exhibited no increase in mortality due to air exposure (up to 60 s; Roth et al. 2018b). Lastly, only a single mortality was reported in steelhead that were captured via angling in the Bulkley River, British Columbia, and exposed to air for up to 30 s (Twardek et al. 2018).

Results of the current study are in concordance with the above studies reporting little to no effect of air exposure on mortality. No effect of air exposure on short-term postspawn survival was observed during either year of our study. Furthermore, no difference in short-term survival was observed between fish that were played and those that were not played or air exposed (NF group) in 2017. The number of out-migrating adults detected in 2016 was lower than that in 2017, which may be attributable to a PIT antenna malfunction (~3 weeks) that likely allowed a substantial portion of the study fish to out-migrate without being detected. Many studies have reported short-term survival of fish exposed to air (e.g., Thompson et al. 2008; Gagne et al. 2017), but ours is the first to evaluate the relative effects of air exposure on fish over the long term. Similar to short-term survival, air exposure had no effect on survival after a full year.

Although much less studied, another potential effect of air exposure on fish is reduced fitness through altered reproductive success. We are aware of only two studies that have attempted to address this question, and the results are contradictory. Richard et al. (2013) used adult Atlantic Salmon that were captured via angling as they traveled upstream to spawn. Once a fish was captured, a tissue sample was collected, and the angler recorded how long the fish was exposed to air during release. After spawning, backpack electrofishing was used to capture age-0 fish that were then assigned back to adult fish to evaluate the relationship between air exposure and production of progeny. Richard et al. (2013) reported that Atlantic Salmon exposed to air for more than 10 s had two to three times lower reproductive success than fish that were not exposed to air. Based on their study, a "10-s rule" was proposed for implementation in all C&R fisheries, where anglers would not be allowed to remove fish from the water for more than 10 s (Cook et al. 2015;

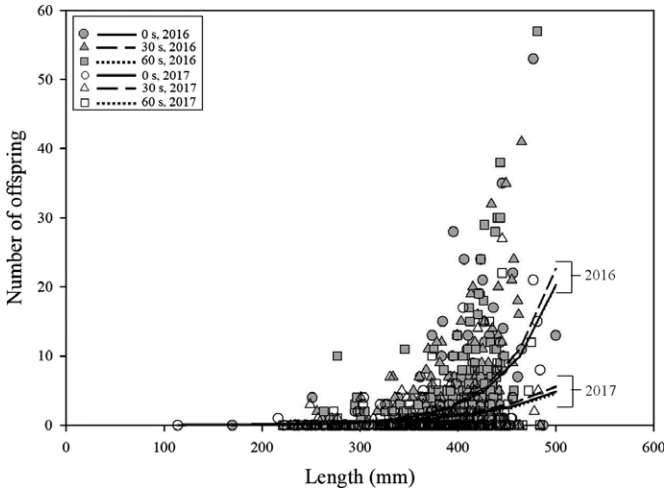

FIGURE 7. Number of offspring produced by adult male Yellowstone Cutthroat Trout in Burns Creek, Idaho (May–October 2016; or May–September 2017), in relation to male TL. Lines represent the predicted number of offspring produced by males belonging to each air exposure treatment group.

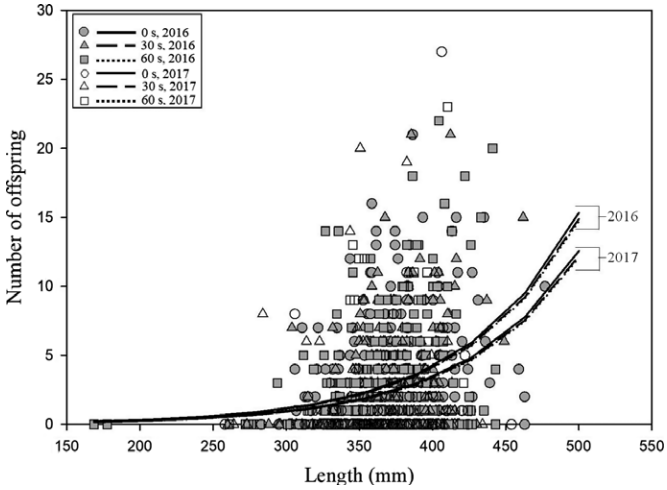

FIGURE 8. Number of offspring produced by adult female Yellowstone Cutthroat Trout in Burns Creek, Idaho (May–October 2016; May–September 2017), in relation to female TL. Lines represent the predicted number of offspring produced by females belonging to each air exposure treatment group.

Twardek et al. 2018). Unfortunately, this recommendation fails to acknowledge the limitations of the Richard et al. (2013) study. Although the work of Richard et al. (2013) was quite novel and innovative, the study suffered from small sample sizes. Only 40 adult Atlantic Salmon were caught and released, and only 24 were exposed to air. Additionally, the authors' analysis indicated that longer exposure to air resulted in increased reproductive success when the water was warm (>17°C) compared to a decline in reproductive success when the water was colder. This observation is contrary to nearly all other studies on the relationship between salmonids and water temperature (Strange et al. 1977; Dotson 1982; Beacham and Murray 1985; Vladic and Jätrvi 1997). In the only other study that has evaluated reproduction and air exposure, no decline in spawning success was observed after simulated capture and up to 60 s of air exposure for Chum Salmon and Pink Salmon (Raby et al. 2013). Those results, along with the current findings, suggest that air exposure experienced during a typical C&R angling event (i.e., <30 s; Lamansky and Meyer 2016; Chiaramonte et al. 2017; Roth et al. 2018b) does not significantly influence reproductive success.

The most obvious pattern in our study was that larger Yellowstone Cutthroat Trout produced more offspring than smaller individuals. Similar patterns have been reported extensively in the literature for a variety of taxa, including salmonids (Bulkley 1967; Riebe et al. 2014). Larger fish produce more and larger eggs than smaller fish (Bulkley 1967). Larger fish also reportedly produce offspring that are more likely to survive due to factors such as better energy resources (yolk) or better habitat conditions selected by larger parents (e.g., large substrates; Palumbi 2004; Marshall et al. 2010; Riebe et al. 2014).

Overall progeny production was seemingly lower in 2017 than in 2016, but lower production of progeny in 2017 can potentially be attributed to differences in streamflow. The 2017 water year was a record year across the basin. For example, discharge in the SFSR averaged 375.1 m^3/s in 2016 during the study period. In 2017, average discharge was nearly 40% higher (520.6 m^3/s). Lower assignment rates of fry to two parents in 2017 were also likely attributable to the high-water year, in which some fish were apparently able to pass the velocity barrier weir on Burns Creek without being captured.

Management Implications

As with any study, the results of the current study are generally limited to the focal species and study system. However, considering that the majority of the literature and the current study report little to no effect of air exposure on mortality or reproductive success for a variety of species, it seems unlikely that exposing fish to air, as currently practiced during C&R angling, is a management problem. This conclusion is based on the available literature describing observed mortality rates in appropriately realistic field experiments and the merging of those study results with the rapidly increasing number of studies documenting air exposure times associated with actual anglers practicing C&R. The latter body of literature suggests that the majority of anglers in a variety of fisheries, including coldwater, coolwater, and warmwater fisheries, release their fish within 30 s (Lamansky and Meyer 2016; Chiaramonte et al. 2017; Roth et al. 2018a; Kevin Meyer, unpublished data). Given the growing collection of evidence, regulations limiting the amount of time that anglers expose fish to air during C&R angling, as have been proposed (Cook et al. 2015), seem unnecessary. Nonetheless, additional studies are warranted to address air exposure concerns in other C&R fisheries, including additional species that may be more sensitive than those studied to date, or in specific systems with elevated water temperatures.

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