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NOTE

Fall and Winter Survival of Brook Trout and Brown Trout in a North-Central Pennsylvania Watershed

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Abstract

Stream-dwelling salmonids that spawn in the fall generally experience their lowest survival during the fall and winter due to behavioral changes associated with spawning and energetic deficiencies during this time of year. We used data from Brook Trout *Salvelinus fontinalis* and Brown Trout *Salmo trutta* implanted with radio transmitters in tributaries of the Hunts Run watershed of north-central Pennsylvania to estimate survival from the fall into the winter seasons (September 2012–February 2013). We examined the effects that individual-level covariates (trout species, size, and movement rates) and stream-level covariates (individual stream and cumulative drainage area of a stream) have on survival. Brook Trout experienced significantly lower survival than Brown Trout, especially in the early fall during their peak spawning period. Besides a significant species effect, none of the other covariates examined influenced survival for either species. A difference in life history between these species, with Brook Trout having a shorter life expectancy than Brown Trout, is likely the primary reason for the lower survival of Brook Trout. However, Brook Trout also spawn earlier in the fall than Brown Trout and low flows during Brook Trout spawning may have resulted in a greater risk of predation for Brook Trout compared with Brown Trout, thereby also contributing to the observed differences in survival between these species. Our estimates of survival can aid parameterization of future population models for Brook Trout and Brown Trout through the spawning season and into winter.

Understanding survival and the mechanisms driving survival of fish populations is important to ecologists and resource management agencies working to conserve and manage populations. For stream-dwelling salmonids that are generally governed by a small number of mature individuals, having a better understanding of individual survival may prove vital in understanding the overall population dynamics and how these populations might respond to climate change (Brook et al. 2008). The fall spawning season represents a stressful time period for fall-spawning salmonid species, and survival tends to be lower during this time of year than during other times of the year (Carlson and Letcher 2003; Petty et al. 2005). Possible mechanisms for decreased survival include energetic deficits combined with changes in behavior associated with spawning. Sweka and Hartman (2008) found that prey consumption and condition (as indexed by energy density) of Brook Trout *Salvelinus fontinalis* in West Virginia streams declined from summer through the fall months. Cunjak et al. (1987) also observed declining condition of Brook Trout in Ontario streams over this time of year. In addition to lower prey energetic acquisition, the energetic demands of spawning result in decreased survival, and Berg et al. (1998) found that repeat-spawning Brown Trout *Salmo trutta* had lower survival than first-time spawners. Individual size may also play a role in survival as predators have displayed size selectivity when preying on salmonids (Osterback et al. 2014). Increased movement associated with spawning behavior of Brook Trout and Brown Trout during the fall (Mollenhauer et al. 2013; Davis et al. 2015) may expose salmonid species to a greater risk of predation compared with other times of the year. Osterback et al. (2013) found that migrants became especially vulnerable when traversing certain landscapes because they allowed for increased feeding efficiency by predators. Moreover, these

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predation effects may be further exacerbated by environmental conditions, such as stream discharge encountered during movements (Antolos et al. 2005; Hostetter et al. 2012). Lastly, although Brown Trout have been naturalized in native Brook Trout streams in Pennsylvania, uncertainties about their influence on Brook Trout still exist. Brown Trout have been documented to out-compete Brook Trout for scarce resting positions (Fausch and White 1981) and preferred pool habitats of limited availability (Modde et al. 1991). These behavioral differences that have proved advantageous for Brown Trout in interactions between the species may also prove advantageous in survival.

Most studies that estimate the survival of stream-dwelling salmonids have used mark–recapture methods and provide a probability of survival from one sampling event to another sampling event some time later (e.g., Mitro and Zale 2002; Carlson and Letcher 2003; Petty et al. 2005). Although mark–recapture methods provide good estimates of survival between points in time and can be used in other population modeling efforts (e.g., Letcher et al. 2007), they lack detail on specifically when mortality events occur. One means to gain greater detail on how mortality changes through time is through the use of telemetry studies. Although advances in telemetry technology have increased the application to a broader suite of species and over longer time periods, studies still may be limited based on tag size and battery life. Telemetry studies on stream-dwelling salmonids have generally been conducted with the objective of evaluating fish movement and habitat use (e.g., Young 1995; Roghair and Dolloff 2005; Petty et al. 2012; Mollenhauer et al. 2013; Davis et al. 2015). Using telemetry data to estimate the survival of animals in terrestrial environments has been common (e.g., Pollock et al. 1989a; Anders et al. 1997; Nicholson et al. 1997; McLellan et al. 1999), but this application of telemetry data is still relatively new in fish populations (recent applications include Hightower et al. 2001; Heupel and Simpfendorfer 2002; Pollock et al. 2004; Ivasauskas and Bettoli 2011; Furey et al. 2016). Survival analysis techniques have also recently been applied when evaluating the passage of fish around migratory barriers (Castro-Santos and Haro 2003). Common to these aforementioned studies is the use of a nonparametric estimator of a survivorship function developed by Kaplan and Meier (1958). The survivorship function estimates the probability of an animal in the population surviving some number of time units from the beginning of the study and is based on the number of animals at risk of death at a given time and the number of known deaths occurring at a given time.

The objective of this analysis was to further examine the data used in Smith (2013) and Davis et al. (2015) (which examined movement and habitat usage of Brook Trout and Brown Trout) to estimate survival of Brook Trout and Brown Trout through the fall season based on radiotelemetry data, representing the period of prespawning to postspawning. We also determined if survival was influenced by covariates representing variation in stream habitat (individual streams and cumulative drainage area) and covariates representing variation among individual fish (species, fish size, and individual movement rate). Assessment of Brook Trout and Brown Trout survival when these species are present in sympatry could also elucidate mechanisms responsible for the decreasing occurrence of native Brook Trout with the establishment of nonnative Brown Trout (Wagner et al. 2013). Such information would be valuable in the conservation of Brook Trout in its native range.

METHODS

Study area.—This study was conducted in multiple streams within the Hunts Run watershed of north-central Pennsylvania (Figure 1). The watershed is heavily forested and the majority is located on publically accessible lands managed by the Pennsylvania Department of Conservation and Natural Resources and has a total watershed area of 79.3 km^2. Study streams consisted of the main stem of Hunts Run (cumulative drainage area of 79.3 km^2) and four tributaries: McKinnon Branch (24.9 km^2), McNuff Branch (14.1 km^2), Rock Run (3.8 km^2), and Whitehead Run (11.3 km^2) (Table 1). All streams had sympatric populations of Brook Trout and Brown Trout except for Rock Run, which had an allopatric Brook Trout population. Hunts Run drains into Driftwood Branch of Sinnemahoning Creek (hereafter referred to as Driftwood Branch).

Implantation of radio transmitters.—A total of 55 Brook Trout and 45 Brown Trout were implanted with radio transmitters between September 13 and September 20, 2012. Details of radio transmitter implantation are provided in Davis et al. (2015) and Smith (2013). Briefly, fish were collected via backpack electrofishing in each of the study streams and we targeted fish that were age 1 and older and likely sexually mature. Fish were anesthetized and radio transmitters were implanted using the shielded-needle technique (Ross and Kleiner 1982), whereby a small incision was made in the abdomen of the fish where the main body of the tag was inserted and the antenna exited the body through a hole created by a hypodermic needle posterior to the incision. The incision was closed with two to three sutures. The radio transmitters used were Lotek (Lotek Wireless, Nemarket, Ontario) NanoTag series digitally coded transmitters (NTC-3-2 1.1 g; 124-d life expectancy, active between 0600 and 1800 hours). Following recovery from implantation of radio transmitters, fish were released within 50 m of their point of capture.

The distribution of implanted fish was as follows: Hunts Run (13 Brook Trout and 17 Brown Trout), McKinnon Branch (10 Brook Trout and 10 Brown Trout), McNuff Branch (8 Brook Trout and 12 Brown Trout), Whitehead Run (14 Brook Trout and 6 Brown Trout), and Rock Run (10 Brook Trout). Because a few trout experienced mortality early in the study

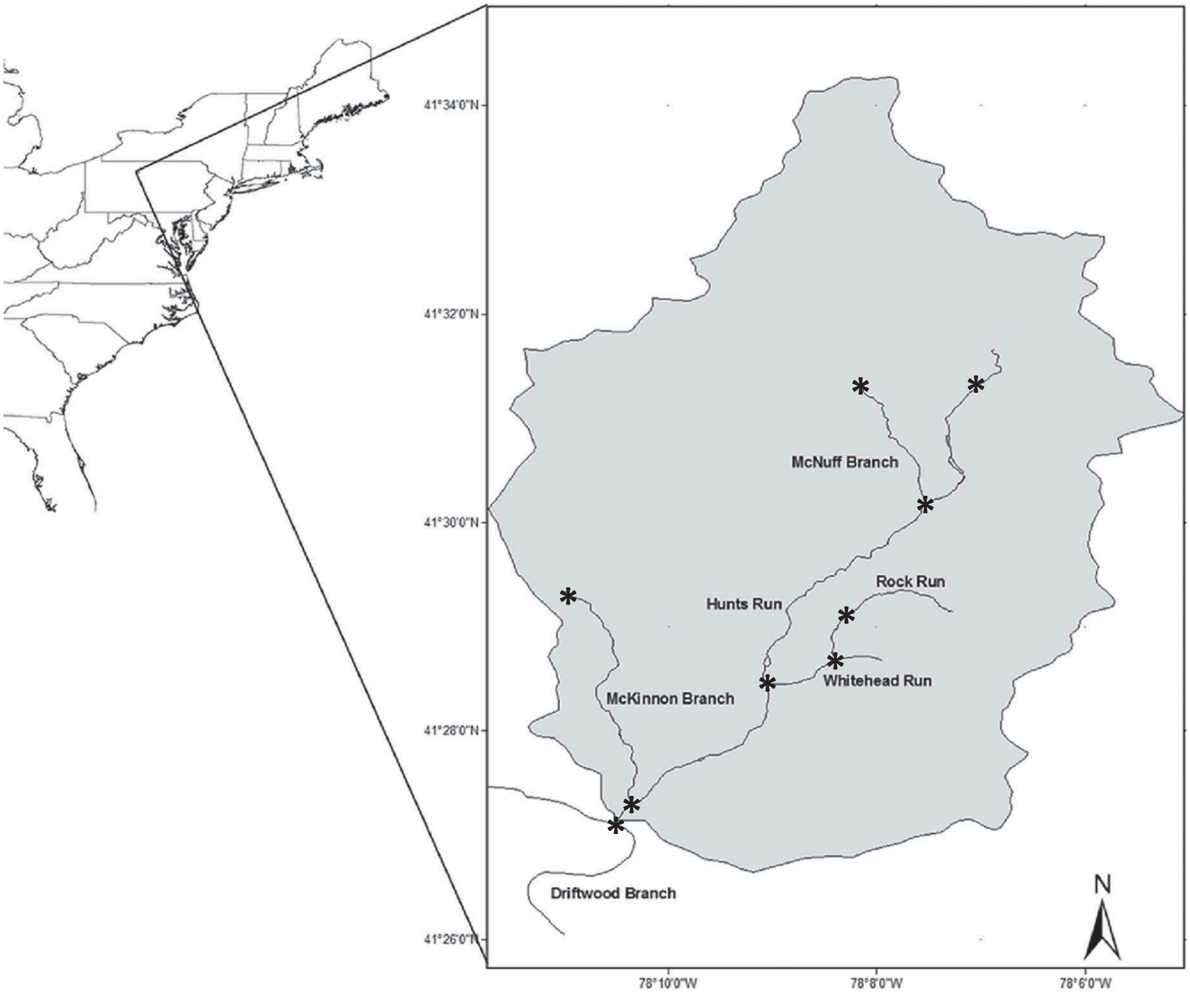

FIGURE 1. Map of Hunts Run watershed showing the stream reaches where Brook Trout and Brown Trout were implanted with radio transmitters. The asterisks indicate the upper and lower limits of the sampling reach within Hunts Run watershed. The lowermost asterisk indicates the confluence of Hunts Run with Driftwood Branch.

and their radio transmitters were recovered, these recovered transmitters were then implanted in four additional Brown Trout in Hunts Run on October 16, 2012. Unfortunately, we did not note the sex or maturity stage of each individual fish in the study, but we believe that nearly all, if not all, were sexually mature based on the size ranges of sexually mature Brook Trout and Brown Trout in the literature (McFadden 1961; Taube 1976; Hutchings 1993). Also, we tagged a random sample of fish greater than the minimum size requirements for the weight of our transmitters (55 g based on a 2% tag : fish weight ratio) and believe this sample was representative of the sex ratio of Brook Trout and Brown Trout present in the watershed.

Radio-tracking.—Tracking fish began on September 16, 2012, and was performed by two crews of two people each (Smith 2013). Crew members located fish during daytime hours and obtained a location on each individual two to three times per week between September and December 2012. When a fish was located, its location was recorded via GPS. After December 2012, fish were located less frequently as movement decreased into the winter season. All tracking ceased after February 25, 2012, due to the battery life of the radio transmitters expiring. When locating a fish, crew members attempted to visually identify the exact location of the fish without disturbing the fish. In cases when researchers were unable to locate fish, either due to mortality or large-scale movements, tracking throughout the instream reaches commenced. This tracking effort resulted in both locating individuals that made large-scale movements as well as locating transmitters outside the stream (Davis et al. 2015). Fish whose transmitters were found outside the stream were considered dead beyond that point and the date was noted.

Statistical analysis.—Survival of Brook Trout and Brown Trout was assessed using a Kaplan–Meier survivorship

TABLE 1. Stream habitat characteristics within the Hunts Run watershed, where Brook Trout and Brown Trout were implanted with radio transmitters. The values for pH represent average values from samples collected between October and December 2012. Specific conductance represents a single point estimate taken in each stream in July 2012. Gradient and percent pool habitat were based on thalweg profiles conducted in the summer of 2012 (Davis and Wagner 2016).

Stream	Stream order	Cumulative drainage area (km^2)	pH	Specific conductance (μs/cm)	Gradient (%)	Percent pool habitat (%)
Hunts Run	4	79.3	6.63	45.1	1.5	47
McKinnon Branch	2	24.9	6.34	27.4	2.1	42
McNuff Branch	2	14.1	6.74	39.4	1.7	32
Rock Run	1	3.8	6.75	34.0	5.4	29
Whitehead Run	2	11.3	7.01	52.5	2.5	33

function (Kaplan and Meier 1958; Pollock et al. 1989a; Krebs 1994) using the OIsurv and KMsurv packages in R (version 3.0.2). The Kaplan–Meier survivorship function estimates the probability of an individual surviving t units of time from the beginning of the study.

$$\hat{S}_t = \prod_{i=1}^{n}\left[1-\left(\frac{d_i}{r_i}\right)\right] \tag{1}$$

and

$$\mathrm{var}\left(\hat{S}_t\right) = \hat{S}_t^2\left[\sum_{i=1}^{n}\left(\frac{d_i}{r_i(r_i-d_i)}\right)\right], \tag{2}$$

where $\hat{S}_t$ is the probability of survival over some time period t, d_i is the number of deaths recorded at time i, r_i is the number of individuals alive and at risk of death at time i, and n is the number of time checks for possible deaths. The Kaplan–Meier survivorship function is advantageous because it allows for a staggered entry design (i.e., individuals entering the study at different times) and allows for censored data when individuals drop out of the study or when an individual's fate is unknown. In this study, the time of entry to the study was the date at which a fish was implanted with a radio transmitter and released. For individuals that suffered mortality during the study, the time of death was the date on which death was confirmed by the tracking crew. Individuals were censored for two reasons: (1) they migrated from the Hunts Run watershed study area to Driftwood Branch or (2) they were no longer located in any area but were also not confirmed as dead (e.g., possible tag battery failure). In both of these cases, the time of censoring was the date on which the last location was made in the Hunts Run watershed. Thus, fish were considered "alive" in this study if they were still swimming around in the study area. To minimize biasing our estimates of survival due to mortality caused by the handling effects of radio transmitter implantation, we omitted any individual fish that was implanted and released but for which no locations were made 24 h after release.

The effects of covariates on Brook Trout and Brown Trout survival were examined using Cox proportional hazards models (Cox 1972; Pollock et al. 1989b). The hazard function is the instantaneous rate of death conditional on survival time and has the following form:

$$h(t|z) = h_0(t)\exp\{\beta' z\}, \tag{3}$$

where $h_0(t)$ is the baseline hazard, z is a vector of covariates, and β' is a vector of parameters similar to regression parameters in a multiple regression model. We first analyzed our survival data with both species combined and used a Cox proportional hazards model to determine if there was a difference in survival among trout species (Brook Trout versus Brown Trout). Cox proportional hazards models were then used to determine if the covariates of stream, cumulative drainage area, fish size (weight), and fish movement rate influenced survival. Separate hazard models were evaluated for each covariate. Individual movement rate was estimated as the cumulative distance moved (m) in both upstream and downstream directions divided by the number of days between release and the last known location (m/d). A nonparametric Wilcoxon rank sum test was used to test for basic differences among Brook Trout and Brown Trout implanted with radio transmitters in terms of size (weight in grams) and movement rates (m/d).

RESULTS

Some individual fish were not located following their release and most were censored prior to the end of the study on February 25, 2012. Two Brook Trout released in Hunts Run and two Brown Trout released in McNuff Branch were not located after their release dates and were not included in survival analyses. The total number of fish included in the survival analyses was 53 Brook Trout and 46 Brown Trout (Table 2). Of the 53 Brook Trout, 17 were confirmed dead during the course of the study and 31 were censored prior to the end of tracking. Of the 46 Brown Trout, 4 were confirmed dead during the course of the study and 41 were censored prior to the end of tracking. Also, 4 Brook Trout and 13 Brown Trout were censored because they migrated downstream out of the Hunts Run watershed and into Driftwood Branch. The maximum number of Brook Trout at risk of death at any point in time during the study was 48, which occurred between September 20 and September 24, 2012. The maximum number of Brown Trout at risk of death was 45, which occurred between October 16 and October 18, 2012 (Figure 2). After mid-January, the number of fish remaining in the study declined rapidly (Figure 2) due to censoring individuals that could no longer be located, likely due to battery failure of the transmitters by that time. By the end of the study on February 25, 2013, only five Brook Trout and one Brown Trout remained at risk. All others were either confirmed dead or censored.

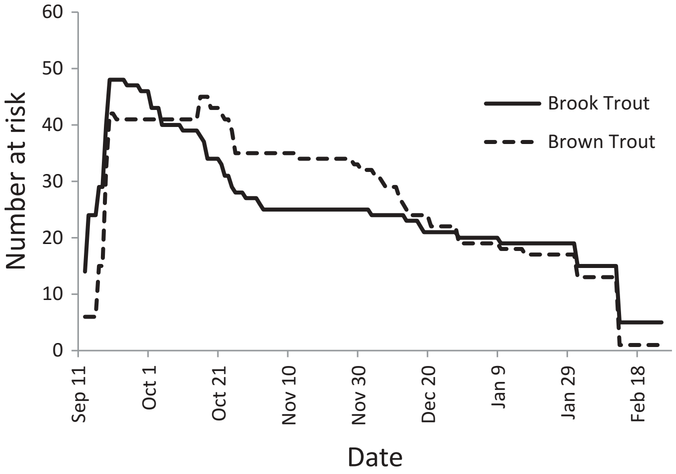

FIGURE 2. Numbers of Brook Trout and Brown Trout at risk of death in the Hunts Run watershed during the course of the study (September 13, 2012, to February 25, 2013). The number at risk on a given date reflects the number removed from the study due to confirmed deaths and censored individuals that were no longer located or who had emigrated downstream out of the watershed and into Driftwood Branch.

The Cox proportional hazards model indicated that there was a significant difference in survival between Brook Trout and Brown Trout (Wald test statistic = 6.99, df = 1, $P = 0.01$). Given this species difference in survival, Kaplan–Meier survivorship functions were then estimated for each trout species separately. Brook Trout survival decreased faster than Brown Trout survival (Figure 3). Brook Trout survival from September 13 to October 31 was 0.66 (95% CL = 0.52–0.83) and survival to the end of the study was 0.56 (0.41–0.74). Thus, the major decline in Brook Trout survival occurred prior to the end of October and survival from November 1 through the end of the study was 0.82 (0.69–0.98). Brown Trout survival from September 13 to October 31 was 0.93 (0.86–1.00), and survival to the end of the study was 0.90 (0.82–0.99). Like Brook Trout, Brown Trout survival did not decrease in the latter part of the study with survival from November 1 to the end of the study at 0.97 (0.92–1.00).

Other than a species effect, none of the other covariates had a significant influence on survival when the data were analyzed with the species combined or separate (Table 3). The species did differ in size ($W = 844$, $P < 0.01$), with the median

TABLE 2. Summary of Brook Trout and Brown Trout implanted with radio transmitters in the Hunts Run watershed in September 2012. The numbers in parentheses correspond to minimum and maximum values.

Species	Stream	Number implanted	Confirmed deaths	Number censored	Median length (mm)	Median weight (g)	Median movement rate (m/d)
Brook Trout	Hunts Run	11	3	5	217 (185–275)	90 (62–210)	17 (0.23–98.40)
	McKinnon Branch	10	1	8	238 (175–345)	133 (49–417)	23 (0.11–59.13)
	McNuff Branch	8	3	5	189 (162–252)	63 (45–146)	12 (4.39–29.94)
	Rock Run	10	2	7	201 (185–230)	77 (71–124)	3 (2.61–6.24)
	Whitehead Run	14	8	6	218 (185–260)	98 (61–175)	3 (0.23–23.59)
Brown Trout	Hunts Run	21	2	18	260 (185–430)	145 (55–829)	10 (0.35–151.24)
	McKinnon Branch	9	1	8	213 (185–345)	88 (51–382)	18 (2.11–53.42)
	McNuff Branch	10	0	10	232 (161–315)	112 (46–267)	6 (0.51–32.33)
	Whitehead Run	6	1	5	231 (170–290)	171 (47–231)	3 (1.17–5.82)

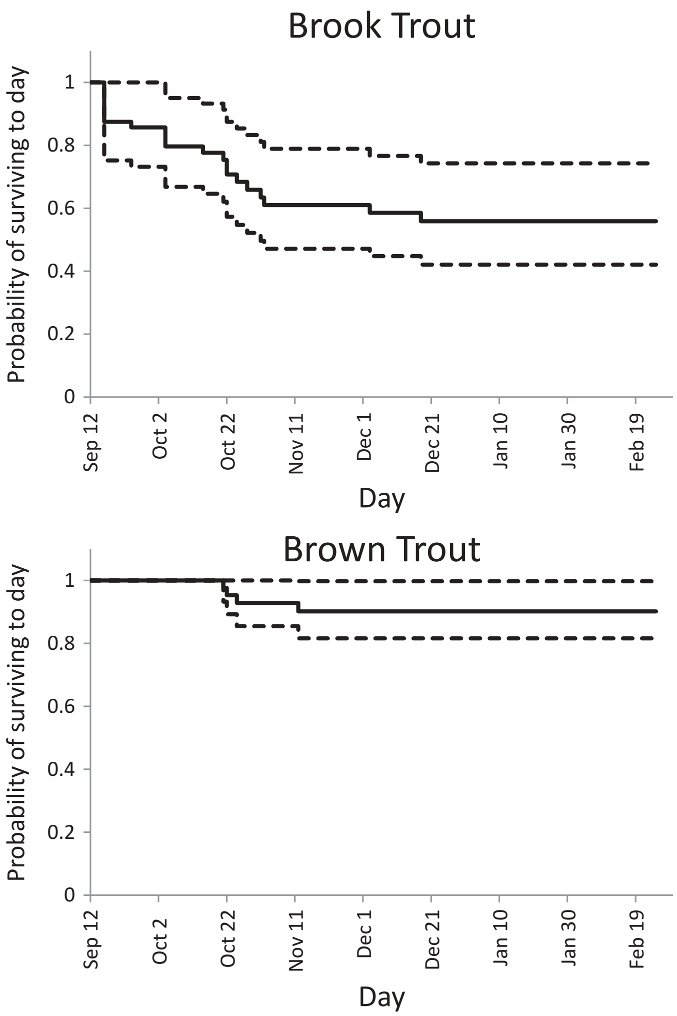

FIGURE 3. Kaplan–Meier survivorship estimates for Brook Trout and Brown Trout in the Hunts Run watershed. The dashed lines represent 95% confidence intervals.

TABLE 3. Test statistics used to evaluate the effects of covariates on Brook Trout and Brown Trout survival in the Hunts Run watershed (September 2012–February 2013).

Species	Covariate	Wald test statistic	df	*P*-value
Combined	Species	6.99	1	0.01
	Stream	5.16	4	0.27
	Cumulative drainage area (km^2)	0.56	1	0.45
	Fish weight	0.96	1	0.33
	Movement rate	0.29	1	0.59
Brook Trout	Stream	3.71	4	0.45
	Cumulative drainage area (km^2)	0.16	1	0.69
	Fish weight	0.27	1	0.61
	Movement rate	0.78	1	0.38
Brown Trout	Stream	0.17	3	0.98
	Cumulative drainage area (km^2)	0.08	1	0.78
	Fish weight	0.03	1	0.86
	Movement rate	0.01	1	0.92

size of Brown Trout equaling 123 g and that of Brook Trout equaling 90 g, but this did not influence survival when the species were combined or examined separately (see Table 3 for test statistics). Movement rates (m/d) did not differ between the species (W = 1,026, P = 0.90) and did not influence survival when the species were combined or separate. Likewise, habitat-related covariates of stream and cumulative drainage area did not influence survival (Table 3).

DISCUSSION

The survival of Brook Trout was markedly lower than the survival of Brown Trout, especially in the early portion of our study, and we examined potential mechanisms responsible for this difference. Although Brown Trout in this study were larger than Brook Trout and all fish received the same size of implanted radio transmitters, it is unlikely that the larger proportional weight of implanted radio transmitters in Brook Trout was a cause for this difference among species. Cox proportional hazard models indicated no effect of the size of the fish on survival for either species separately or when the species were combined. Movement rates also did not differ among the species and had no influence on the survival of either species. We expected to see those fish with greater movement also having lower survival as greater movement could increase their exposure and increase their risk of predation (potential predators in our study area included the following: great blue heron *Ardea herodias*, belted kingfisher *Megaceryle alcyon*, American mink *Neovison vison*, raccoon *Procyon lotor*, and northern water snake *Nerodia sipedon*). Both species were distributed among all streams (except for Rock Run, which had an allopatric Brook Trout population), yet individual stream and cumulative drainage area were not correlated with survival of either species. The relatively low sample size of implanted fish within each stream and the resulting low statistical power may be partly responsible for the lack of any observed differences in survival among streams.

The most simplistic explanation for the differences in survival among Brook Trout and Brown Trout is the difference in life history among these species in Pennsylvania streams. Brook Trout in Pennsylvania streams mature at age 1–2 and can live for 3–4 years (Detar 2007), whereas Brown Trout mature at age 2–3 and live for 5–7 years (McFadden and Cooper 1962; Bachman 1984). Although differences in life expectancy may explain why Brook Trout had lower survival estimates than Brown Trout, the large difference in survival between Brook Trout and Brown Trout in this study (0.56 compared with 0.82, respectively, over the entire study) suggests that behavioral mechanisms that were not explicitly measured by this study may have also contributed to the difference in survival between these trout species.

The spawning period for Brook Trout in Pennsylvania streams typically begins in mid-September and extends through early November (Wydoski and Cooper 1966), whereas the spawning period of Brown Trout is shifted later in the year, from the end of October through mid-December (Beard and Carline 1991). Both species select similar spawning habitat with coarse substrate, typically found in the tails of pools. However, the timing of spawning for each of these species places them in this habitat under different flow conditions and water depths. October typically has lower flows than November in Pennsylvania streams, and this was certainly the case during the time of our telemetry data collection (Smith 2013). We noticed during tracking that spawning Brook Trout were much more visible under the low-flow conditions of October than spawning Brown Trout were later in the season under higher-flow conditions. Thus, we speculate that in addition to differences in life history between these species, peak spawning activity by Brook Trout during October when flows were low, and the associated greater risk of predation during this time, also contributed to the much lower survival of Brook Trout. Brook Trout also showed less avoidance behavior when approached by tracking crews.

A large proportion of the fish implanted with transmitters were censored by the end of the study (58% of Brook Trout and 89% of Brown Trout). The reason for the high proportion of censored individuals is simply because the batteries of the transmitters began to fail. The expected battery life of the transmitters was 124 d, and we saw a rapid decline in the number of fish that were still able to be located after mid-January. The high censoring rate towards the end of the study did not compromise our estimates of survival because all confirmed deaths of Brook Trout and Brown Trout occurred prior to when the life expectancy of the batteries was expected to begin expiring. The attractiveness of the Kaplan–Meier survivorship estimator is that it accommodates censored individuals, and even if we only analyzed data until the last confirmed death of either species (December 18 for Brook Trout and November 12 for Brown Trout), estimates of survival up until those points in time would be the same.

As previously stated, most studies that estimate survival of stream-dwelling salmonids do so through the use of mark–recapture methods and have concluded that survival is lower from fall to spring than it is from spring to fall (Hunt 1969; Hutchings 1993; Quinn and Peterson 1996; Mitro and Zale 2002; Carlson and Letcher 2003; Petty et al. 2005). Our estimate of overall survival of Brook Trout from the beginning to the end of our telemetry study (0.56) is slightly higher than other estimates of Brook Trout survival over equivalent time periods. Carlson and Letcher (2003) estimated age-1+ fall survival ranging from 0.35 to 0.44 from fall into early winter, and Petty et al. (2005) estimated Brook Trout survival from fall to spring of 0.31. Also, McFadden (1961) estimated overwinter Brook Trout survival ranging from 0.37 to 0.57 in a Wisconsin stream. Estimates of Brook Trout survival from Carlson and Letcher (2003) and Petty et al. (2005) are apparent survival, which does not account for emigration from their study sites, whereas our ability to censor individuals that emigrated from the Hunts Run Watershed did. Carline (2006) estimated annual Brown Trout survival in a Pennsylvania stream from 0.25 to 0.70, and if our estimate of Brown Trout survival over our five and a half month study was extrapolated to an entire year, it would fall within this range.

Our analysis of survival of Brook Trout and Brown Trout is unique in that the use of radiotelemetry allowed continual estimates of survival from the fall into winter, rather a single estimate of survival between two discrete points in time. For Brook Trout and Brown Trout in this study, the majority of the mortality occurred around the time of spawning, and there was minimal mortality following spawning and the onset of winter. These estimates of survival could be used in other population models for these species to add more realism to those models. For example, rather than having a single estimate of survival from fall to spring, modelers could stipulate a lower survival value during the period of spawning, followed by a higher survival value postspawn.

The lower survival of Brook Trout compared with that of Brown Trout is most likely due to differences in life history, with Brook Trout having a shorter life expectancy than Brown Trout, but we also speculate that flow conditions during the expected peak spawning periods of each species may add to the differences in survival. Our study was limited in that it was only conducted over a single spawning season, and we thus cannot fully examine how variation in stream flow influences survival. Losses in Brook Trout habitat as a function of increasing water temperature have been predicted throughout the native range of Brook Trout, and these losses may be further exacerbated given changes in precipitation patterns that could occur as a result of climate change (Deweber 2014). While the relationship of how these habitat losses will translate into actual survival is unknown, future telemetry studies repeated over multiple spawning seasons will be valuable in developing improved population models and decision making to conserve native Brook Trout in the face of climate change and nonnative competitors such as Brown Trout.

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