Transactions of the American Fisheries Society 139:1360–1371, 2010

DOI: 10.1577/T09-010.1

[Article]

Annual Intrabasin Movement and Mortality of Adult Bonneville Cutthroat Trout among Complementary Riverine Habitats

ANDREW J. CARLSON[1]* AND FRANK J. RAHEL

Department of Zoology and Physiology, University of Wyoming, Department 3166,
1000 East University Avenue, Laramie, Wyoming 82071-3166, USA

Abstract.—We evaluated annual movement and mortality patterns of native Bonneville cutthroat trout *Oncorhynchus clarkii utah* in the Smiths Fork–Bear River watershed, which is part of the Great Basin in the western USA. Our objectives were to identify complementary habitats within the watershed, identify sources of mortality for Bonneville cutthroat trout during seasonal movements, and determine whether anthropogenic structures disrupt movement of adult Bonneville cutthroat trout within this system. Bonneville cutthroat trout migrated upstream during spring runoff (median distance = 37.1 km) and experienced a seasonal mortality rate of 43% during this period. After spawning in the headwater streams, fish moved downstream during the summer–autumn period (median distance = 11.6 km) and experienced a seasonal mortality rate of 16%. Whereas upstream movement in the spring was fast and highly directed, downstream movement during summer–autumn was slower and less directed. During winter, fish remained generally sedentary (median movement upstream = 0.1 km) and the seasonal mortality rate was 11%. No anthropogenic structures blocked fish movement throughout the watershed. However, an irrigation canal entrained 9% of the fish that moved past its headgate, suggesting that the canal may act as an ecological trap. Our results provide empirical support for conceptual models that emphasize the importance of habitat complementarity as the basis for annual long-distance movement patterns in riverine fishes. Managing migratory species such as the Bonneville cutthroat trout will require maintaining river connectivity and minimizing ecological traps so that fish can move among widely separated habitats to meet their life history requirements.

Movement between different areas is common in many species of fish (Lucas and Baras 2001). This movement provides fish an opportunity to exploit new resources, escape inhospitable conditions, or avoid predation. To understand the reasons for such movements, conceptual models have emphasized the importance of habitat complementarity—the idea that no single habitat can satisfy all of the ecological and life history requirements of a species (Schlosser 1991; Dunning et al. 1992; Northcote 1997). The basic premise of these models is that optimal habitat for a species varies (1) across life history stages, (2) with seasonal changes in abiotic conditions or resource availability, or (3) in response to interactions with other species. Thus, to maximize survival, growth, and reproduction, fish species often need to move among contrasting habitats.

Often, movements are over short distances that are considered to be within the home range of the individual (Dingle 1996). Such movements allow fish to exploit spatially variable food resources or minimize interactions with competitors or predators (Gowan and Fausch 2002). In addition to short-distance movements, there can be directed movements that cover longer distances that extend beyond the home range. These long-distance movements are often associated with spawning events and may result in movement to areas with different habitat conditions compared with where the fish normally resides. These directed, undistracted movements exhibited by many riverine fishes are known as migrations (Dingle 1996).

Depending on the species and system, movement among complementary habitats can have ecological tradeoffs. Anadromous and semelparous fish perish after spawning in freshwater systems, and even iteroparous fish can have high mortality rates associated with spawning migrations (e.g., Vinyard and Winzeler 2000; Narum et al. 2008). Additionally, anthropogenic breaks in the riverscape (e.g., dams or seasonal dewatering in the system) may disrupt movement among habitats (Schlosser 1995; Fausch et al. 2002), potentially negating the benefits associated with a migratory life history. As research and management paradigms shift from emphasizing small areas and short time periods to considering multiple scales that include large geographical areas and long time periods, concepts such as connectivity, landscape patchiness, and large-scale ecological changes become important for understanding the complex life history

---

* Corresponding author: andrew.carlson@state.mn.us

[1] Present address: Minnesota Department of Natural Resources, Section of Fisheries, 1601 Minnesota Drive, Brainerd, Minnesota 56401, USA.

Received January 20, 2009; accepted May 3, 2010

and ecology of species within riverine systems (Fausch et al. 2002).

For some fish species, life history strategies may involve movements across large spatial extents (Dunham and Rieman 1999; Rieman and Dunham 2000; Lucas and Baras 2001). There has been particular interest in examining such movements by inland salmonids because of concerns that anthropogenic activities may be fragmenting habitat and harming many populations (Schmetterling 2003; Schrank and Rahel 2004; Colyer et al. 2005; Gale et al. 2008). However, because of the logistic difficulties and expense of monitoring fish movements over long distances and time periods, most studies have focused on movement within a single season or in association with spawning migrations (Brown and Mackay 1995a, 1995b; Jakober et al. 1998; Schmetterling 2001, 2003; Meka et al. 2003; Schrank and Rahel 2004, 2006; Colyer et al. 2005). Studies that encompass longer time periods are needed if we are to understand the full extent of fish migrations in riverine systems and relate movement patterns to the conceptual framework emphasizing habitat complementarity. Whereas the benefits of moving among complementary habitats are often stressed, we also need to consider the costs, especially as related to increased mortality risk.

We evaluated movement patterns for a population of native Bonneville cutthroat trout *Oncorhynchus clarkii utah* (hereafter, cutthroat trout). Our study took place within the Bear River and a major tributary, the Smiths Fork, which are part of the Great Basin of the western United States. The Bear River and lower elevations of the Smiths Fork are used for irrigated agriculture, and summer temperatures and water quality can reach suboptimal levels for salmonids (Colyer et al. 2005). Earlier work in this system focused on postspawning movement (Schrank and Rahel 2004, 2006) and winter movement (Colyer et al. 2005) of cutthroat trout. This prior work documented that the life history of cutthroat trout in the system often involves movements among complementary habitats, with adults spawning in headwater tributaries and juveniles out-migrating from these tributaries at age 1 (90–120 mm; Colyer and Harig 2004). Our work extends these studies by evaluating the annual movement cycle of large adults among complementary habitats and determining the mortality associated with these movements. Our objectives were to (1) relate movement patterns of adult cutthroat trout within the Smiths Fork–Bear River system to conceptual models of habitat complementarity and (2) identify sources of cutthroat trout mortality during the seasonal movements within this system.

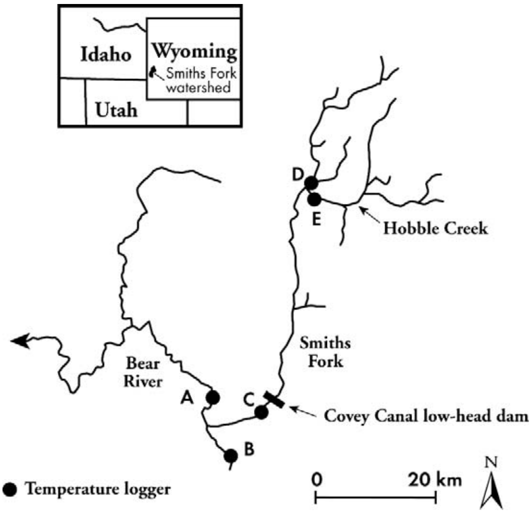

FIGURE 1.—Smiths Fork drainage in southwest Wyoming, showing the Covey Canal low-head dam and the locations of temperature loggers (A = Bear River downstream from the Smiths Fork confluence; B = Bear River upstream from the Smiths Fork confluence; C = Smiths Fork upstream from the Bear River confluence; D = Smiths Fork upstream from the Hobble Creek confluence; E = Hobble Creek upstream from the Smiths Fork confluence). Inset shows general location of the study area in southwest Wyoming.

Methods

Study site.—The Smiths Fork in Lincoln County, Wyoming, is one of the largest tributaries to the Bear River in the Great Basin (Figure 1). The Smiths Fork watershed is 708 km^2, and headwater streams originate in the Wyoming Range of the Rocky Mountains. At mid-elevations, the watershed is characterized by a partly forested mountain landscape with steep valleys. At lower elevations, the watershed transitions into broad irrigated valleys. Discharge varies throughout the year, with a large increase in streamflow associated with snowmelt beginning between late March and mid-April and a return to base flows during midsummer (Figure 2). The climate is characterized by long, cold winters and hot, dry summers; mean annual precipitation is 33 cm.

An average of 32% of the annual flow in the Smiths Fork is removed for irrigation use by a series of canals throughout the basin, with as much as 78% of the flow removed during the peak of the irrigation season (Figure 2). As fish move through the lower part of the watershed during the irrigation season, they can become entrained in these canals (Carlson and Rahel 2007; Roberts and Rahel 2008). Cutthroat trout and mountain whitefish *Prosopium williamsoni* are the only native salmonids in the Smiths Fork–Bear River

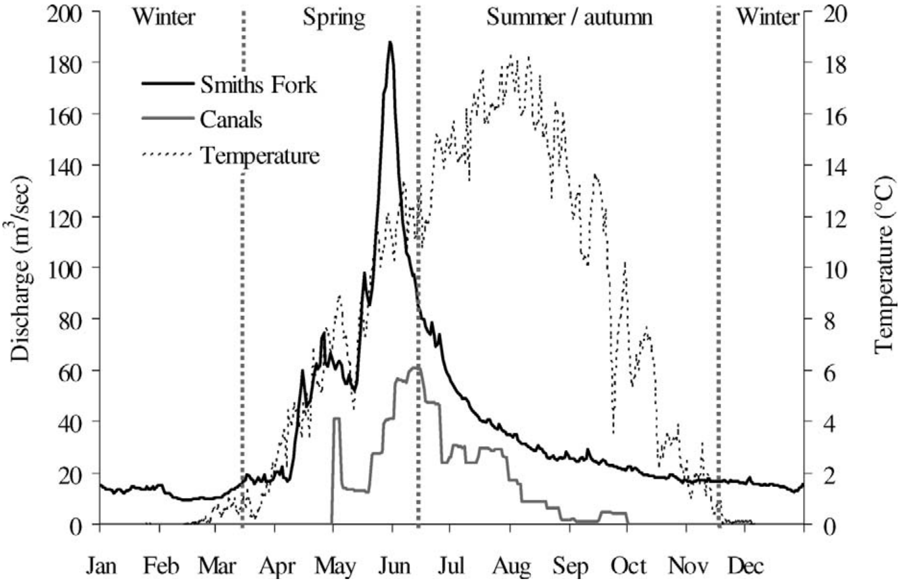

FIGURE 2.—Hydrograph and thermograph of the Smiths Fork (daily averages from U.S. Geological Survey gauge 10032000 and from temperature logger C in Figure 1) and the water withdrawn by the canals throughout the watershed in 2003. Overlain are the seasonal periods that delineate the timing of Bonneville cutthroat trout movements.

system. The only other salmonids present are naturalized brown trout *Salmo trutta*.

Radiotelemetry.—Radiotelemetry was used to monitor seasonal movements of adult cutthroat trout between August 2003 and August 2006. We used four types of pulsed radio tags and one type of digital radio tag (see Table A.1 for tag specifications) to provide maximum battery life for various sizes of fish while keeping the transmitter weight under 2% of body weight for tagged individuals (Winter 1983). Transmitters were surgically implanted into cutthroat trout following the methodology described by Adams et al. (1998). Fish were collected (mean total length = 387 mm; range = 319–495 mm; 55% male) and received implanted transmitters at locations throughout the basin during late spring (1 May to 15 June, $N = 83$) and summer–autumn (15 July to 1 November, $N = 56$). Fish were implanted with radio transmitters and minimally tracked at 1-month intervals during the summer. Fish were located on the ground using either an R2000 receiver (Advanced Telemetry Systems, Isanti, Minnesota) or an SRX_400 receiver (Lotek Wireless, Newmarket, Ontario) with a three-element Yagi antenna (Advanced Telemetry Systems). Where detection was possible from a road, scanning was done from a vehicle. On sections of river without nearby roads, the section of river was scanned by walking. During the remainder of the year, bimonthly tracking surveys were conducted on the ground or from a fixed-wing aircraft outfitted with at least two directional "H" antennas (one on each wing; additional details in Roberts and Rahel 2005). The flight path covered the entire study area (including canal systems) illustrated in Figure 1 and additionally continued upstream on the Bear River to Pixley Dam (25.5 river kilometers [rkm] upstream from the Smiths Fork confluence) and downstream on the Bear River to a site near Pegram, Idaho (57.8 rkm downstream from the Smiths Fork confluence), covering an average distance of 320 km. Fish located with the fixed-wing aircraft were subsequently tracked on the ground to verify their locations and to provide more precise location data. When a fish was located, its position was recorded using a Global Positioning System unit (eTrex Venture; Garmin, Olathe, Kansas) along the streambank. Each radio transmitter was equipped with a mortality sensor so that we could determine whether fish were still alive. Fish locations were entered into geographical information system software (ArcView 3.3; Environmental Systems Research Institute [ESRI], Redlands, California). Each fish location was assigned a river meter measured upstream from the confluence of the Smiths Fork and the Bear River using the Network Analyst (ESRI) and the Shortest Network Paths extension (Neudecker 1999).

Seasonal time periods.—We used several sources of information to delineate three seasonal time periods: spring, summer–autumn, and winter. These periods were based on previous studies of cutthroat trout movement in the Bear River system (Hilderbrand and Kershner 2000; Colyer et al. 2005) and on seasonal cues, such as rising or falling water temperatures, flow, or both, which influenced fish movement during preliminary observations of radio-tagged cutthroat trout. The spring period began as water temperatures and discharge increased with the onset of spring runoff in mid-March. The spring period ended in mid-June, when average daily water temperatures reached approximately 10°C (the upper limit of Bonneville cutthroat trout spawning activity; Kershner 1995). The summer–autumn period extended from mid-June to mid-November, when average daily water temperatures dropped below 4°C. Brown (1999) indicated that cutthroat trout *O. clarkii* reduced their activity at temperatures below 4°C. The winter period began in mid-November and continued until the initiation of the spring period the following year.

Objective 1: movement patterns between complementary habitats.—We used the locations of radio-tagged fish to assess seasonal movement patterns. Movement distances were calculated only for fish that survived for 3 weeks postsurgery; this was done to eliminate fish whose behavior may have been affected by the surgical procedure (Pickering et al. 1982). For each fish that was alive at 3 weeks postsurgery, we associated each location with a season. For the 62 fish that were located multiple times during at least one season, we calculated the maximum displacement distance (km) as the difference between the farthest upstream location and farthest downstream location of a fish within a season; positive values indicated upstream movement, and negative values indicated downstream movement. We calculated a standardized movement rate (m/d) by dividing the displacement distance by the number of days that had elapsed. Because the displacement distances within a season and the standardized movement rates were not normally distributed (Kolmogorov–Smirnov test: $P < 0.05$) and did not have equal variances (Levene's test: $P < 0.05$), we used nonparametric analyses. Confidence intervals (95%) for medians were calculated using the binominal distribution. To compare movement distances among seasons, we used a Kruskal–Wallis test with a post hoc multiple comparison and the Bonferroni adjustment (Zar 1999). All analyses were conducted in the Statistical Analysis System version 9.1 (SAS Institute, Cary, North Carolina), and statistical significance was determined using an α of 0.05.

To further examine seasonal differences in movement patterns, we used linear regression to determine the relationship between the displacement distance within a seasonal period and the number of elapsed days between fish locations. If fish remained stationary or moved quickly to a new location and then remained stationary, we would expect no relationship between displacement distances and elapsed days. If fish moved incrementally within a season, we would expect a positive slope coefficient for upstream movement and a negative slope coefficient for downstream movement.

We were able to track eight radio-tagged cutthroat trout through a continuous annual cycle. To compare the median seasonal movement distances of these eight fish with movement distances of the remaining fish (i.e., those followed through one or two seasons), we used a Mann–Whitney two-sample test (Zar 1999). This allowed us to determine whether the movement patterns of fish followed for one or two seasons were similar to the movement patterns of fish followed through an annual cycle.

We evaluated the degree of habitat complementarity by quantifying stream habitat characteristics in relation to stream order (Strahler 1957). Our study area contained a fifth-order stream (the Bear River), a fourth-order stream (main stem of the Smiths Fork below the confluence with Hobble Creek), two third-order streams (Hobble Creek and the Smiths Fork above the confluence with Hobble Creek), and numerous second- and first-order headwater streams in the Smiths Fork watershed (Figure 1). Average stream wetted width and maximum pool depth were measured during summer low-flow conditions (20 July to 19 August 2005). Wetted width was measured at a minimum of 50 locations within each stream order category. The entire lengths of second- to fifth-order tributaries and a subset of first-order tributaries (those where radio-tagged cutthroat trout were found) were evaluated to find the maximum pool depth per stream order. Deep pools are known to be an important habitat component for cutthroat trout, especially during winter (Brown and Mackay 1995b; Colyer et al. 2005). Maximum pool depth was measured using a 1- or 4-m standing rod. Temperature was measured using recorders (HOBO Water Temp Pro V2; Onset Computer Corporation, Bourne, Massachusetts) placed throughout the basin in second- to fifth-order streams. Temperature was recorded every 30 min and summarized for a period of maximum summer temperatures (20 July to 19 August 2005). The average slope for each stream order was derived from a U.S. Geological Survey digital elevation model with 10-m horizontal resolution and 1-m vertical resolution. For each stream order category, 50 random points were selected along the stream segments with a minimum separation of 250 m, and the elevation was obtained from the digital elevation model at the random point and then at another point 200 m downstream. The elevation at the upper point was then subtracted from the elevation at the lower point and divided by 200 to yield an estimate of stream slope.

Objective 2: identify sources of mortality for cutthroat trout during seasonal movements.—We attempted to identify seasonal patterns in the magnitude and sources of mortality. When a radio transmitter emitted a mortality signal, we attempted to retrieve the transmitter and determine the most probable source of mortality. When transmitters were recovered from mustelid dens, those fish were assumed to have been killed by a mustelid. When transmitters were recovered from great blue heron *Ardea herodias* rookeries or below bald eagle *Haliaeetus leucocephalus* nests, the fish were assumed to have been killed by those predators. To explore the interaction between predation and canal entrainment, we determined whether the last known location of cutthroat trout that became prey was within or outside of the canal system. Fish that were entrained in and later perished in the canals were considered canal-related mortalities. Fish with transmitters that were returned by anglers were considered to be angling mortalities. Mortality that could not be attributed to one of the above causes was categorized as being due to unknown causes.

To explore the interaction between predation and canal entrainment, we determined whether the last known location of fish that suffered predation mortality was within or outside of the canal system. We calculated the seasonal mortality rate by dividing the number of mortalities observed during each season by the number of fish that were alive at the beginning of the season.

Results

Objective 1: Movement Patterns among Complementary Habitats

We obtained a minimum of two locations for 16 cutthroat trout during the winter period, 38 fish during the spring spawning migration, and 53 fish during the summer–autumn period (Table A.2). There were distinct patterns of movement among complementary habitats (Figure 3). During winter, cutthroat trout were sedentary. During spring, cutthroat trout showed extensive upstream movements toward headwater spawning tributaries. These movements were fast and highly directed. By contrast, movement during the summer–autumn period was slower and less directed and occurred in a downstream direction. There were statistically significant differences in displacement distances (Kruskal–Wallis test: $F = 86.35$; df = 2, 104; $P < 0.001$) and standardized movement rates (Kruskal–Wallis test: $F = 84.02$; df = 2, 104; $P < 0.001$) across seasons. The displacement distances and standardized movement rates were significantly different among all seasons (post hoc multiple comparisons using a Bonferroni adjustment: $P \leq 0.001$).

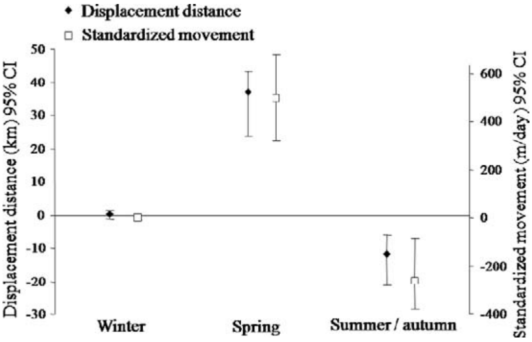

FIGURE 3.—Seasonal displacement distances and standardized movement rates (medians with 95% confidence intervals [CIs]) of Bonneville cutthroat trout in the Smiths Fork–Bear River system. The differences in displacement distances and standardized movement rates were significant among all seasons ($P \leq 0.001$).

The differences in seasonal movement patterns were particularly evident in a subset of eight fish tracked for a 1-year period (Figure 4). These fish spent the winter in low-elevation reaches (fourth- and fifth-order streams), migrated to headwater streams to spawn (first- and second-order streams), and then returned to mid-elevation reaches to spend the summer–autumn (third- and fourth-order streams). Comparison of these eight fish with the other radio-tagged fish indicated that the displacement distances and standardized movement rates were not significantly different during the winter, spring, or summer–autumn (Mann–Whitney two-sample test: $P > 0.05$). Thus, movement of fish followed through an annual cycle was similar to that of fish followed for one or two seasons.

To further examine seasonal differences in movement patterns, we regressed the displacement distance within a seasonal period against the number of elapsed days between fish locations. The relationship was not significant for the winter period ($P = 0.62$), thus reflecting the overall lack of movement of fish during this season. The relationship also was not significant for the spring period ($P = 0.20$), which reflects the highly directed and fast nature of the spring spawning migration. Cutthroat trout tended to move from winter locations to spawning locations over a relatively short period and then remained in the spawning tributaries. In contrast to results for the other two seasons, there was a statistically significant relationship between displacement distance and the number of days between locations during the summer–autumn period ($P = 0.02$;

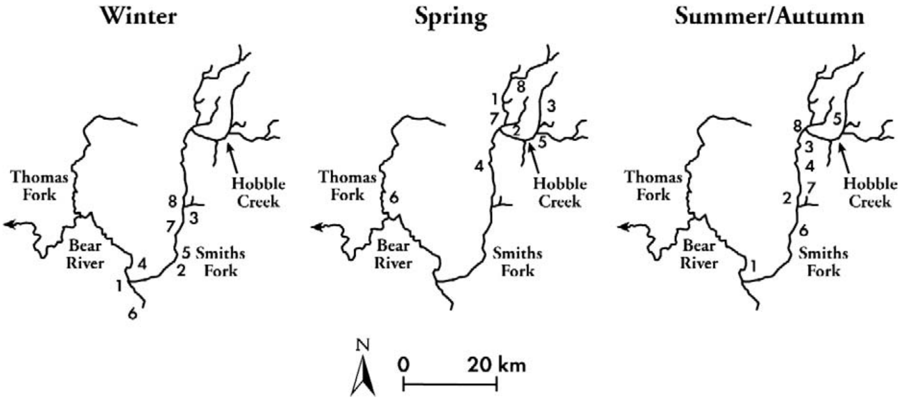

FIGURE 4.—Locations of eight radio-tagged Bonneville cutthroat trout followed through the Smiths Fork–Bear River system over an annual period. Numbers identify individual fish.

$y = -0.22x - 8.68$, where y is fish displacement distance [km] and x is the number of elapsed days). This relationship suggests that fish were continually moving downstream throughout the summer–autumn. Based on the above regression equation, the downstream distance moved by a fish during the 139-d summer–autumn period would be 39.2 km, which is essentially equal to the median distance that fish moved upstream during the spring (37.1 km).

There were clear differences in stream habitat characteristics among stream orders. Average stream width and maximum pool depth increased with stream order, indicating an increase in overall habitat volume in lower-elevation stream segments (Figure 5). Average reach gradient declined with stream order, reflecting the transition from high-gradient headwater streams in the Rocky Mountains to low-gradient streams at low elevations. Summer temperature increased with stream order, reflecting the 1,100-m decline in elevation from headwater streams to the Bear River.

Objective 2: Sources of Cutthroat Trout Mortality during Seasonal Movements

Over the 3 years of the study, 139 radio transmitters were implanted into cutthroat trout. Of these radio-tagged fish, 36 died within 3 weeks of surgery and were not included in the analysis. Of the remaining 103 radio-tagged fish, 9 fish were still alive at the completion of the study, 41 fish were confirmed mortalities, and the fate of the remaining 53 fish was unknown. For many of these 53 fish, it is likely that the batteries in the transmitters expired. It is also possible that some of the tagged fish may have migrated or were moved out of the study area. The 41 fish for which mortality was confirmed lived an average (±SE) of 204 ± 19 d after surgery. The seasonal mortality rate based on these 41 fish was considerably higher during the spring period (43%) than in the winter (11%) or summer–autumn period (16%; Table 1). On an annual basis, 70% (29) of the 41 confirmed mortalities occurred during the spring period. Predation by great blue herons accounted for 20% of the mortalities and was concentrated in the spring, when fish were spawning in shallow tributary streams. All radio-tagged fish that became prey were preyed upon outside of the canals, suggesting that predation was not just due to entrainment. Angler harvest accounted for 15% of the mortalities. This estimate may be conservative due to underreporting, even though we publicized our study with landowners and local fishers and asked that tags from angled fish be returned.

We identified only one anthropogenic feature that may have impeded trout movement: a low-head dam across the Smiths Fork that directs water toward the headgate of the Covey Canal (Figure 1). The dam creates a 0.3-m drop into a downstream pool that is minimally 1 m deep under base flow conditions. Across the crest of the diversion structure, water velocity averages (±SE) 0.97 ± 0.3 m/s during base flow conditions. No cutthroat trout were found in the same location within 100 m upstream or downstream of this feature when located on different dates, indicating that the cutthroat trout were not congregating at the structure. All 13 cutthroat trout that approached the dam while moving upstream passed over it, but two individuals were subsequently entrained in the Covey Canal. Of the 33 fish that approached the dam while moving downstream, 31 fish passed over the dam, but two entered the Covey Canal. Thus, 9% (4) of the 46 fish that moved past the canal headgate subsequently

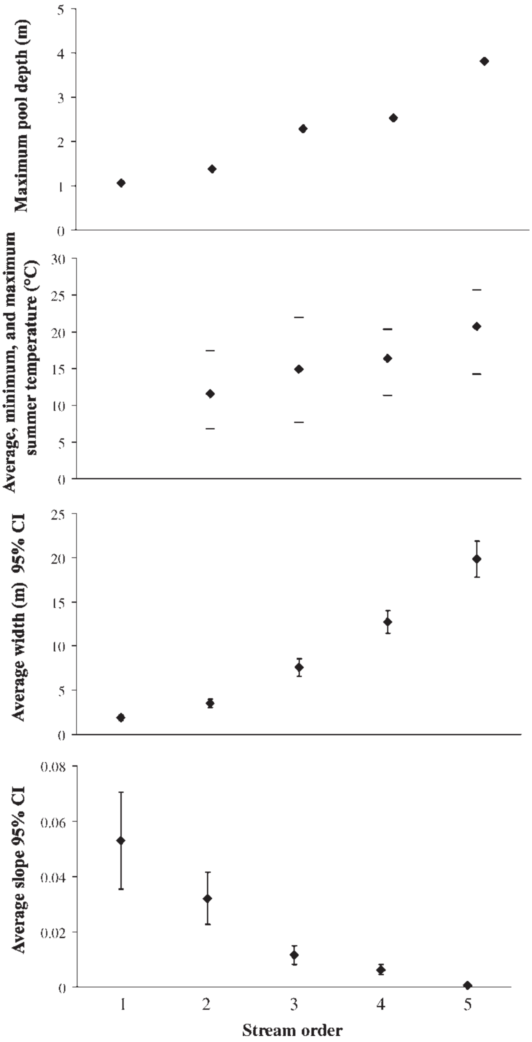

FIGURE 5.—Relationship between stream order and (1) maximum pool depth, (2) summer water temperatures (average, minimum, and maximum), (3) average stream width (with 95% confidence interval [CI]), and (4) average reach gradient (slope; with 95% CI) in the Smiths Fork–Bear River basin.

became entrained in the canal and experienced disruption of their migration.

Discussion

Adult cutthroat trout in the Smiths Fork–Bear River demonstrate annual movement patterns that allow the use of complementary habitats located in widely separated portions of the watershed. Fish moved extensive distances upstream in the spring in a relatively short time period to headwater tributaries, where they remained for a period of weeks engaged in confirmed spawning activities. Cutthroat trout then returned downstream to main-stem habitat in the Smiths Fork over an extended period of time during the summer and autumn. By late autumn, many of these fish had migrated downstream to the Bear River, which contained the deepest pools in the basin. Once stream temperatures dropped during late autumn, the fish remained relatively sedentary throughout the winter.

These movement patterns provide quantitative support for widely cited conceptual models that attribute fish movement to the necessity of exploiting complementary habitats to meet different life history requirements (Figure 6). Cutthroat trout spawn in streams with silt-free gravel and small cobble substrates, which are usually found in headwater tributaries (Magee et al. 1996). Although we did not quantify stream substrates, the high gradients in headwater tributaries move sand and silt through the system, exposing the gravel and cobble that are necessary for spawning by cutthroat trout (Hubert and Kozel 1993). Because headwater streams are also small (as evidenced by the narrow widths of first- and second-order streams), they typically lack the deep pools that provide refuge from mammalian or avian predators. In fact, much of the annual mortality we observed for cutthroat trout occurred during the spring period (Table 1), and we commonly observed great blue herons foraging in streams that contained spawning fish. Most adult cutthroat trout returned downstream after spawning (Schrank and Rahel 2004), and it seems likely that this movement is due to the lack of pool habitat in headwater streams. In fact, creation of pool habitat in these streams resulted in an increased in adult cutthroat trout (Binns and Remmick 1994).

Summer habitat for adult cutthroat trout in our system seems to be concentrated in mid-order stream segments, such as the main-stem Smiths Fork, where deep pools provide refuge from mammalian and avian predators and where stream temperatures remain cool enough for trout. Summer habitat in segments farther downstream, such as the Bear River, appears to be limited by high water temperatures. Daily average water temperatures in the Bear River were close to 22°C, which is near the upper lethal limit for cutthroat trout (Johnstone and Rahel 2003). Migratory brown trout in northeast Wisconsin exhibited similar movement patterns, utilizing deepwater downstream habitats in the winter and spring but moving to cooler upstream areas when stream temperatures became unfavorable during the summer (Meyers et al. 1992). During winter, trout generally reduce their activity at cold temperatures and often seek refuge in deep pools where current velocities are low (e.g., Brown and Mackay 1995b;

TABLE 1.—Seasonal patterns and sources of mortality for radio-tagged Bonneville cutthroat trout in the Smiths Fork–Bear River system, Wyoming–Idaho.

Variable	Winter	Spring	Summer–autumn	Total	Mortality source (%)
Number of fish alive at start of period	18	67	63		
Number of fish dying during period	2	9	10	41	
Seasonal mortality (%)	11	43	16		
Source of mortality:					
Mustelid predation	0	2	1	3	7
Great blue heron predation	1	7	0	8	20
Bald eagle predation	0	0	1	1	2
Canal entrainment	0	2	1	3	7
Angler harvest	0	2	4	6	15
Unknown	1	16	3	20	49

Colyer et al. 2005) and the risk of predation from endothermic predators is reduced (Lonzarich and Quinn 1995). In our system, such habitat was present in the Bear River, and many cutthroat trout moved downstream to this area and spent the winter in deepwater habitat, where they were relatively inactive.

Differences in movement rates among seasons provide additional perspective on the degree to which movements were specifically directed to a certain area. Fish moved upstream during the spawning migration almost twice as fast as their downstream movement after spawning (Figure 3). The median standardized movement upstream during the spawning migration was 496 m/d, which is probably a conservative estimate because the time between locations was minimally 1 month and fish could have moved from downstream winter areas to upstream spawning areas over a much shorter time period. Schmetterling (2001) found that the migrations of westslope cutthroat trout *O. clarkii lewisi* to the spawning areas took a maximum of 28 d, resulting in a median daily rate of about 700 m/d. After spawning, most fish did not return immediately to their prespawning locations and many perished; these observations are similar to what we observed during our study.

Whereas others have also found high levels of mortality associated with spring spawning (Brown and Mackay 1995a; Vinyard and Winzeler 2000; Schmetterling 2001, 2003), the contribution of this mortality source to the total annual mortality rate is seldom known. In the Bear River system, the total annual mortality rate for adult cutthroat trout was estimated to be about 50% (Carlson and Rahel 2007), and data from the present study suggest that a high percentage (70%) of this mortality is associated with the spring spawning migration. Predation appears to be an important source of mortality during the spawning season, and fish can be especially vulnerable in low-water years (Brown and Mackay 1995a; Schmetterling 2001). Others have found that mustelids (Jakober et al. 1998), great blue herons (Schmetterling 2001), and other fish (Schmetterling 2001) are predators of spawning fish.

In our study, a high percentage of mortalities were associated with avian predation and angler harvest (Table 1). Most studies of avian predation on fish populations have focused on lakes, reservoirs, or larger river systems where predation by diving birds can be substantial, especially for hatchery-origin trout. For example, up to 31% of rainbow trout *O. mykiss* stocked into a southern Utah reservoir were consumed by diving birds (Modde et al. 1996). Further, Derby and Lovvorn (1997) estimated that birds consumed 80% of the rainbow and cutthroat trout stocked in the North Platte River, Wyoming. Predation by wading birds can also be substantial in fish farms. At trout rearing facilities in the northeastern United States, great blue herons consumed as many as 39% of the hatchery fish

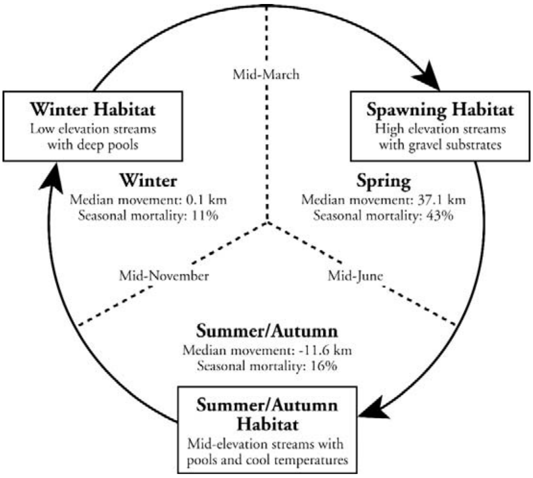

FIGURE 6.—Conceptual model depicting seasonal migrations of Bonneville cutthroat trout among complementary habitats in the Smiths Fork–Bear River system. Upstream movements are denoted by positive distances, and downstream movements are denoted by negative distances.

(Glahn et al. 1999). However, we could find no studies that estimated losses of wild trout to predation by wading birds during the period when large adult trout are in small streams to spawn. Our data suggest that spawning in small tributary streams poses a significant risk of avian predation for large cutthroat trout.

Angler harvest accounted for 15% of the observed mortality of radio-tagged cutthroat trout in the Smiths Fork–Bear River system (Table 1). Similar to our findings, studies in Montana documented that angler harvest accounted for 17% and 20% of the observed mortality of radio-tagged westslope cutthroat trout (Schmetterling 2001, 2003). Whereas avian predation was concentrated in headwater tributaries during the spring spawning season, angler harvest occurred mainly in mid-elevation stream reaches during the summer and autumn.

The extent to which the seasonal mortality patterns or mortality causes are biased is unknown. We assumed that the probability of finding transmitters from dead fish was equal across seasons, but differences in streamflow or ice-cover conditions may influence the likelihood of locating transmitters in unknown ways. We also assumed an equal probability of finding transmitters regardless of the cause of death, but this assumption could be violated if anglers fail to return transmitters or if birds fly to roosting sites far away from the stream. Despite these uncertainties, we believe our data provide insight about major patterns in the timing and causes of mortality for cutthroat trout in the study system.

We did not identify any anthropogenic barriers to cutthroat trout movement in the Smiths Fork basin. The low-head dam associated with the Covey Canal did not impede upstream movement. All fish that approached the diversion dam from the downstream side were located on the upstream side 1–35 d later. The low height of the dam, the moderate water velocities across the crest, and the depth of the downstream plunge pool should have facilitated relatively easy passage for trout (Kondratieff and Myrick 2006). However, 9% of cutthroat trout that migrated past the canal headgate became entrained in the irrigation canal. Previous work in the Smiths Fork indicated a high mortality rate (77%) for cutthroat trout entrained in the Covey Canal (Roberts and Rahel 2008). The canal appears to be acting as an attractive sink habitat (Delibes et al. 2001) that mimics a tributary stream or side channel but becomes lethal when water inflows are terminated. Mortality of fish entrained in irrigation canals or regulated floodplains is common (King and O'Connor 2007; Gale et al. 2008; Jones and Stuart 2008). Discouraging entrainment in sink habitats or providing escape routes becomes an important consideration for managing fish that must move between distant, complementary habitats. Although entrainment may involve only a small number of adult fish when considered at the basin scale (Carlson and Rahel 2007), it is selective against migratory life histories that are part of the evolutionary legacy of many cutthroat trout populations.

Our results provide empirical support for conceptual models suggesting that habitat complementarity is the basis for movement patterns of many riverine fishes (e.g., Schlosser 1991; Fausch et al. 2002). In some cases, complementary habitats may be in close proximity. For example, adults may live in the main stem of a river but move to adjacent backwater habitats to reproduce (Freund and Hartman 2005); alternatively, adults may spawn and spend the summer in main-stem habitat but use backwaters to overwinter (Dauwalter and Fisher 2008). Some minnows and darters spend the summer in riffles but move to adjacent pools to overwinter (Ensign et al. 1997). In our study system, there is evidence that some large adult cutthroat trout are not migratory but instead remain in small tributary streams throughout the year (Sepulveda et al. 2009). These fish move from high-gradient reaches, where they spawn in the spring, to nearby low-gradient reaches to spend the rest of the year in pool habitat (Schrank and Rahel 2004). In these situations, the focus of management efforts should be on maintaining or improving the quality of these adjacent but complementary habitats. For example, enhancing pool habitat in stream segments that contain spawning habitat can increase the abundance of adult trout (Binns and Remmick 1994; White and Rahel 2008).

In other cases, complementary habitats may be located far apart in the landscape. This is the case for cutthroat trout in the Smiths Fork–Bear River system and for many other riverine trout populations (Meyers et al. 1992; Schmetterling 2001, 2003; Meka et al. 2003). In these situations, the focus of management efforts should be on maintaining habitat connectivity and avoiding the creation of ecological traps (e.g., canals) that entice fish into habitat that is ultimately unsuitable for meeting their life history needs.

Acknowledgments

William Baker, Pete Cavalli, Lance East, Kenneth Gerow, Wayne Hubert, Neil Hymas, Dirk Miller, Jon Phillips, James Roberts, Kristin Thompson, and Roy Whaley assisted with this research. Kristin Thompson, Daniel Dauwalter, Al Zale, and two anonymous reviewers provided valuable insights on the manuscript. We thank the landowners in the Smiths Fork–Bear River system for allowing access to study sites. The Wyoming Game and Fish Department provided funding for this project through the State Wildlife Grant Program; the Department of Zoology and Physiology at the University of Wyoming also provided funding.

References

Adams, N. S., D. W. Rondorf, S. D. Evans, and J. E. Kelly. 1998. Effects of surgically and gastrically implanted radio transmitters on growth and feeding behavior of juvenile Chinook salmon. Transactions of the American Fisheries Society 127:128–136.

Binns, N. A., and R. Remmick. 1994. Response of Bonneville cutthroat trout and their habitat to drainage-wide habitat management on Huff Creek, Wyoming. North American Journal of Fish Management 14:669–680.

Brown, R. S. 1999. Fall and early winter movements of cutthroat trout, *Oncorhynchus clarki*, in relation to water temperature and ice conditions in Dutch Creek, Alberta. Environmental Biology of Fishes 55:359–368.

Brown, R. S., and W. C. Mackay. 1995a. Spawning ecology of cutthroat trout (*Oncorhynchus clarkii*) in the Ram River, Alberta. Canadian Journal of Fisheries and Aquatic Sciences 52:983–992.

Brown, R. S., and W. C. Mackay. 1995b. Fall and winter movements of and habitat use by cutthroat trout in the Ram River, Alberta. Transactions of the American Fisheries Society 124:873–885.

Carlson, A. J., and F. J. Rahel. 2007. A basin-wide perspective on entrainment of fish in irrigation canals. Transactions of the American Fisheries Society 136:1335–1343.

Colyer, W., and A. Harig. 2004. Post-spawn movements and juvenile outmigration of fluvial Bear River Bonneville cutthroat trout in Hobble Creek, Wyoming. Wyoming Game and Fish Department, Annual Report, Cheyenne.

Colyer, W. T., J. L. Kershner, and R. H. Hilderbrand. 2005. Movements of fluvial Bonneville cutthroat trout in the Thomas Fork of the Bear River, Idaho-Wyoming. North American Journal of Fisheries Management 25:954–963.

Dauwalter, D. C., and W. L. Fisher. 2008. Spatial and temporal patterns in stream habitat and smallmouth bass populations in eastern Oklahoma. Transactions of the American Fisheries Society 137:1072–1088.

Delibes, M., P. Ferreras, and P. Gaona. 2001. Attractive sinks or how behavioral decisions determine source-sink dynamics. Ecology Letters 4:401–403.

Derby, C. E., and J. R. Lovvorn. 1997. Predation on fish by cormorants and pelicans in a cold-water river: a field and modeling study. Canadian Journal of Fisheries and Aquatic Sciences 54:1480–1493.

Dingle, H. 1996. Migration: the biology of life on the move. Oxford University Press, Oxford, UK.

Dunham, J. B., and B. E. Rieman. 1999. Metapopulation structure of bull trout: influences of physical, biotic and geometrical landscape characteristics. Ecological Applications 9:642–655.

Dunning, J. B., B. J. Danielson, and H. R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. Oikos 65:169–175.

Ensign, W. E., K. N. Leftwich, P. L. Angermeier, and C. A. Dolloff. 1997. Factors influencing stream fish recovery following a large-scale disturbance. Transactions of the American Fisheries Society 126:895–907.

Fausch, K. D., C. E. Torgersen, C. V. Baxter, and H. W. Li. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. Bioscience 52:483–498.

Freund, J. G., and K. J. Hartman. 2005. Largemouth bass habitat interactions among off-channel and main river habitats in an Ohio River navigation pool. Journal of Freshwater Ecology 20:735–742.

Gale, S. B., A. V. Zale, and C. G. Guy. 2008. Effectiveness of fish screens to prevent entrainment of westslope cutthroat trout into irrigation canals. North American Journal of Fisheries Management 28:1541–1553.

Glahn, J. F., T. Tomsa, and K. J. Preusser. 1999. Impact of great blue heron predation at trout-rearing facilities in the northeastern United States. North American Journal of Aquaculture 61:349–354.

Gowan, C., and K. D. Fausch. 2002. Why do foraging stream salmonids move during the summer? Environmental Biology of Fish 64:139–153.

Hilderbrand, R. H., and J. L. Kershner. 2000. Movement patterns of stream-resident cutthroat trout in Beaver Creek, Idaho-Utah. Transactions of the American Fisheries Society 129:1160–1170.

Hubert, W. A., and S. J. Kozel. 1993. Quantitative relations of physical habitat features to channel slope and discharge in unaltered mountain streams. Journal of Freshwater Ecology 8:177–183.

Jakober, M. J., T. E. McMahon, R. F. Thurow, and C. G. Clancy. 1998. Role of stream ice on fall and winter movements and habitat use by bull trout and cutthroat trout in Montana headwater streams. Transactions of the American Fisheries Society 127:223–235.

Johnstone, H. C., and F. J. Rahel. 2003. Assessing temperature tolerance of cutthroat trout based on constant and cycling thermal regimes. Transactions of the American Fishery Society 132:92–99.

Jones, M. J., and I. G. Stuart. 2008. Regulated floodplains—a trap for unwary fish. Fisheries Management and Ecology 15:71–79.

Kershner, J. L. 1995. Bonneville cutthroat trout. Pages 28–35 *in* M. K. Young, editor. Conservation assessment for inland cutthroat trout. U.S. Forest Service General Technical Report RM-256.

King, A. J., and J. P. O'Connor. 2007. Native fish entrapment in irrigation systems: a step towards understanding the significance of the problem. Ecology Management and Restoration 8:32–37.

Kondratieff, M. C., and C. A. Myrick. 2006. How high can brook trout jump? A laboratory evaluation of brook trout jumping performance. Transactions of the American Fisheries Society 135:361–370.

Lonzarich, D. G., and T. P. Quinn. 1995. Experimental evidence for the effect of depth and structure on the distribution, growth, and survival of stream fishes. Canadian Journal of Zoology 73:2223–2230.

Lucas, M. C., and E. Baras. 2001. Migration of freshwater fishes. Blackwell Scientific Publications, Oxford, UK.

Magee, J. P., T. E. McMahon, and R. F. Thurow. 1996. Spatial variation in spawning habitat of cutthroat trout in a sediment-rich stream basin. Transactions of the American Fisheries Society 125:768–779.

Meka, J. M., E. E. Knudsen, D. C. Douglas, and R. B. Benter. 2003. Variable migratory patterns of different adult rainbow trout life history types in a southwest Alaska watershed. Transactions of the American Fisheries Society 132:717–732.

Meyers, L. S., T. F. Thuemler, and G. W. Kornely. 1992. Seasonal movements of brown trout in northeast Wisconsin. North American Journal of Fisheries Management 12:433–441.

Modde, T., A. F. Wasowicz, and D. K. Hepworth. 1996. Cormorant and grebe predation on rainbow trout stocked in a southern Utah reservoir. North American Journal of Fisheries Management 16:388–394.

Narum, S. R., D. Hatch, A. J. Talbot, P. Moran, and M. S. Powell. 2008. Iteroparity in complex mating systems of steelhead *Oncorhynchus mykiss* (Walbaum). Journal of Fish Biology 72:45–60.

Neudecker, K. 1999. Shortest network paths (version 9th September 1999), October 1999 (15 November 2005). Available: arcscripts.esri.com/details.asp?dbid=10028. (January 2009).

Northcote, T. G. 1997. Why sea-run? An exploration into the migratory/residency spectrum of coastal cutthroat trout. Pages 20–26 *in* J. D. Hall, P. A. Bisson, and R. E. Gresswell, editors. Sea-run cutthroat trout: management and future conservation. American Fisheries Society, Oregon Chapter, Corvallis.

Pickering, A. D., T. G. Pottinger, and P. Christie. 1982. Recovery of the brown trout, *Salmo trutta* L., from acute handling stress: a time-course study. Journal of Fish Biology 20:229–244.

Rieman, B. E., and J. B. Dunham. 2000. Metapopulations and salmonids: a synthesis of life history patterns and empirical observations. Ecology of Freshwater Fish 9:51–64.

Roberts, J. J., and F. J. Rahel. 2005. Accuracy of aerial telemetry in fisheries studies. North American Journal of Fisheries Management 25:660–666.

Roberts, J. J., and F. J. Rahel. 2008. Effects of irrigation canals on Bonneville cutthroat trout and other fishes in the Smiths Fork of the Bear River, Wyoming. Transactions of the American Fishery Society 137:951–961.

Schlosser, I. J. 1991. Stream fish ecology: a landscape perspective. Bioscience 41:704–712.

Schlosser, I. J. 1995. Critical landscape attributes that influence fish population dynamics in headwater streams. Hydrobiologia 303:71–81.

Schmetterling, D. A. 2001. Seasonal movements of fluvial westslope cutthroat trout in the Blackfoot River drainage, Montana. North American Journal of Fisheries Management 21:507–520.

Schmetterling, D. A. 2003. Reconnecting a fragmented river: movements of westslope cutthroat trout and bull trout after transport over Milltown Dam. North American Journal of Fisheries Management 23:721–731.

Schrank, A. J., and F. J. Rahel. 2004. Movement patterns in inland cutthroat trout (*Oncorhynchus clarkii utah*): management and conservation implication. Canadian Journal of Fisheries and Aquatic Sciences 61:1528–1537.

Schrank, A. J., and F. J. Rahel. 2006. Factors influencing summer movement patterns of Bonneville cutthroat trout (*Oncorhynchus clarkii utah*). Canadian Journal of Fisheries and Aquatic Sciences 63:660–669.

Sepulveda, A. J., W. T. Colyer, W. H. Lowe, and M. R. Vinson. 2009. Using nitrogen stable isotopes to detect long-distance movement in a threatened cutthroat trout (*Oncorhynchus clarkii utah*). Canadian Journal of Fisheries and Aquatic Sciences 66:672–682.

Strahler, A. N. 1957. Quantitative analysis of watershed geomorphology. Transactions of the American Geophysical Union 38:913–920.

Vinyard, G. L., and A. Winzeler. 2000. Lahontan cutthroat trout (*Oncorhynchus clarkii henshawi*) spawning and downstream migration of juveniles into Summit Lake, Nevada. Western North American Naturalist 60:333–341.

White, S. M., and F. J. Rahel. 2008. Complementation of habitats for cutthroat trout *Oncorhynchus clarkii,* in watersheds influenced by beaver, livestock, and drought. Transactions of the American Fisheries Society 137:881–894.

Winter, J. D. 1983. Underwater biotelemetry. Pages 371–395 *in* L. A. Nielsen and J. D. Johnsen, editors. Fisheries techniques. American Fisheries Society, Bethesda, Maryland.

Zar, J. H. 1999. Biostatistical analysis, 4th edition. Prentice Hall, Upper Saddle River, New Jersey.

Appendix: Additional Information on Radio Tags and Tagging of Bonneville Cutthroat Trout

TABLE A.1.—Specifications of radio tags used to evaluate movement and mortality of Bonneville cutthroat trout in the Smiths Fork–Bear River watershed, Wyoming–Idaho (ATS = Advanced Telemetry Systems).

Pulsed or digital	Dry weight (g)	Pulse or burst rate	Duty cycle	Manufacturer	Battery life (d)	Model
Pulsed	3.5	40 pulses/min	No	ATS	200	357
Pulsed	3.1	50 pulses/min	No	ATS	160	F1570
Pulsed	8.0	50 pulses/min	12/12	ATS	322	F1820
Pulsed	8.9	50 pulses/min	6/18	ATS	520	F1820
Digital	9.0	5 and 5.5 s	6/18	Lotek	483–501	SR-M11–18

TABLE A.2.—Timing and number of observations used to calculate seasonal movements of radio-tagged Bonneville cutthroat trout in the Smiths Fork–Bear River watershed, Wyoming–Idaho. Timing is divided by seasonal time period (summer–autumn [S–A], winter, and spring) among the 4 years of data collection. Each dot represents a minimum of two locations during that season (ID = identification number).

	Fish ID																														
Season and year	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
S–A 2003	•	•	•	•	•	•	•	•	•	•	•	•																			
Winter 2003–2004													•	•	•	•															
Spring 2004	•	•	•										•	•	•	•	•	•	•	•	•										
S–A 2004	•	•											•	•	•		•	•		•	•	•	•	•	•	•					
Winter 2004–2005																											•				
Spring 2005																											•	•	•	•	•
S–A 2005																											•	•			
Winter 2005–2006																															
Spring 2006																															
S–A 2006																															

TABLE A.2.—Continued.

	Fish ID																														
Season and year	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62
S–A 2003																															
Winter 2003–2004																															
Spring 2004																															
S–A 2004																															
Winter 2004–2005																															
Spring 2005	•	•	•	•	•																										
S–A 2005	•					•	•	•	•	•	•	•	•	•	•	•	•	•													
Winter 2005–2006						•	•	•											•	•	•	•	•	•	•	•	•				
Spring 2006						•			•	•									•	•	•	•	•	•	•	•	•	•	•	•	•
S–A 2006																			•	•	•	•	•		•	•	•	•	•		•