

Generation-scale movement patterns of cutthroat trout (*Oncorhynchus clarkii pleuriticus*) in a stream network

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Abstract: Movements by stream fishes have long been the subject of study and controversy. Although much discussion has focused on what proportion of fish adopt mobility within particular life stages, a larger issue involves the lifetime movements of individuals. I evaluated movements of different sizes and ages of Colorado River cutthroat trout (*Oncorhynchus clarkii pleuriticus*) using a variety of sampling methods from 1996 to 2001 in a 40 km network of main-stem and tributary segments of the North Fork Little Snake River, Wyoming, USA. The probability of movement was related to the period of observation, initial location, and possibly individual growth rate, whereas distance moved was related to fish size and initial location. Furthermore, it appeared that movements by juveniles were mostly downstream, whereas those of older fish were largely upstream. Movement of cutthroat trout in this basin appeared to be driven by ontogenetic changes in habitat use and variation in habitat productivity. Given that this stream network exemplifies the complexity typical of many mountain watersheds, movement as a life history tactic in fishes may be more common than is sometimes recognized.

Résumé : Les déplacements des poissons d'eau courante ont depuis longtemps été l'objet d'études et de controverses. Bien qu'une partie importante de la discussion ait porté sur la proportion de poissons qui deviennent mobiles aux différents stades de leur cycle, un problème plus large concerne les déplacements des individus au cours de leur vie entière. Une variété de méthodes d'échantillonnage de 1996 à 2001 sur un réseau de 40 km de segments du cours principal et des tributaires de la North Fork de la rivière Little Snake, Wyoming, É.-U., a permis d'évaluer les déplacements des truites fardées du Colorado (*Oncorhynchus clarkii pleuriticus*) de différents âges et tailles. La probabilité de déplacement est liée à la période d'observation, à l'emplacement initial et possiblement aussi au taux individuel de croissance, alors que la distance du déplacement est reliée à la taille du poisson et à la position initiale. De plus, il semble que les déplacements des juvéniles se font surtout vers l'aval, alors que ceux des poissons plus vieux ont lieu en grande partie vers l'amont. Les déplacements de la truite fardée dans le bassin semblent s'expliquer par des changements ontogénétiques dans l'utilisation des habitats et par la variation dans la productivité de ces habitats. Comme ce réseau hydrographique est un exemple typique de la complexité de plusieurs bassins versants de montagne, le déplacement comme tactique au cours du cycle biologique des poissons pourrait être beaucoup plus répandu qu'on le reconnaît quelquefois.

[Traduit par la Rédaction]

Introduction

Movements of stream fishes have been scrutinized by biologists for decades. Early work (e.g., Shetter and Hazzard 1939) suggested that such movements might be commonplace, but many studies in the 1950s and thereafter concluded that movements of stream fishes were relatively limited, occasionally to single habitats for much or all of the life cycle (Miller 1957; Funk 1957; Gerking 1959). More recent research, relying on radiotelemetry (Clapp et al. 1990), two-way weirs (Gowan and Fausch 1996b), improved fish marking techniques (McCutcheon et al. 1994), otolith microchemistry (Kennedy et al. 2002), genetic markers (Neville et al. 2006), larger spatial and temporal scales (Baxter 2002), and

more rigorous experimental designs (Albanese et al. 2003), has reemphasized the ubiquity of movements in freshwater fish life histories, particularly in stream-dwelling salmonids. Nevertheless, interpreting the frequency and extent of these movements, as well as what proportion of a population undertakes them, remains controversial (Gowan et al. 1994; Rodríguez 2002). We also lack a consistent terminology for describing fish movement (Larson et al. 2002; Holyoak et al. 2008), which contributes to the lack of consensus on how far fish must move to be considered mobile (Gerking 1959; Crook 2004).

Often, marking studies repeatedly capture many individuals in the same location and few individuals in new locations. Although methodological problems can overemphasize this pattern (Porter and Dooley 1993; Koenig et al. 1996), its prevalence contributes to the perspective that stream fish populations often comprise two components: a majority that is sedentary and a minority that exhibits some degree of mobility (Stott 1967; Solomon and Templeton 1976). This apparent dichotomy in behavior is consistent with the leptokurtosis of many stream fish movement distributions (Skalski and Gilliam 2000), and there is some support that it

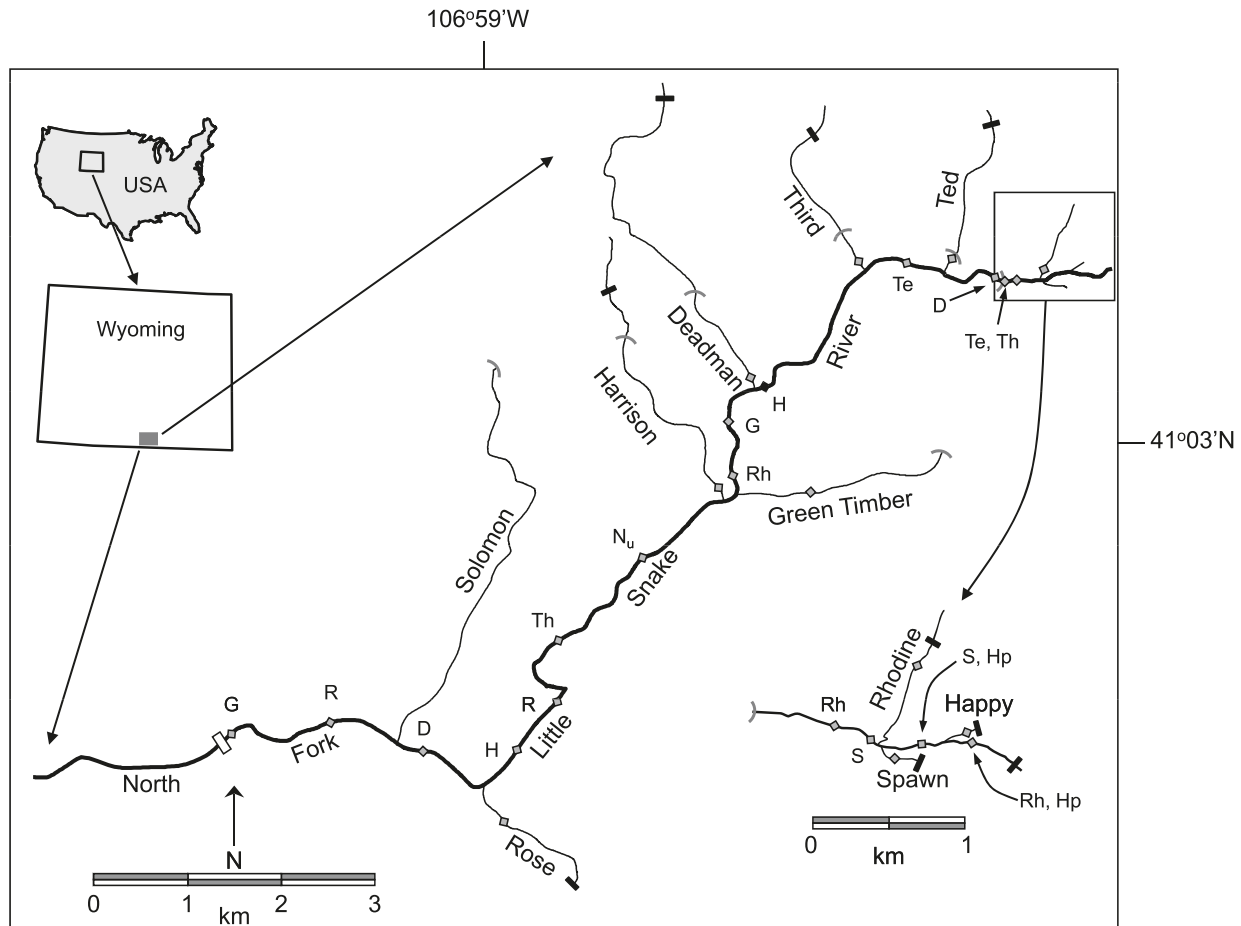
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Fig. 1. The North Fork Little Snake River basin in south-central Wyoming, USA. The arcs denote water diversions, the open bar shows a weir blocking upstream fish migration on the lower main stem, and solid bars indicate the upstream extent of fish (except where terminated by water diversions). Unlabeled diamonds on tributaries represent the upstream-most extent of tagged fish that also used the lower main stem (main panel) or upper main stem (inset). Labeled diamonds on the lower or upper main stem represent the downstream- and upstream-most extent of tagged fish that also were captured in a tributary. Tributary labels: R, Rose; H, Harrison; G, Green Timber; D, Deadman; Th, Third; Te, Ted; Nu, upper North Fork Little Snake; Rh, Rhodine; S, Spawn; and Hp, Happy.



has a behavioral or physiological basis (Fraser et al. 2001; Morinville and Rasmussen 2003). Still, the validity of the mobile-sedentary split is uncertain because most assessments of fish movements are limited to relatively brief (≤ 1 year) intervals (see Rodríguez 2002 for a summary), often rely on methods that preclude evaluations of all age classes (Steingrímsson and Grant 2003), and by definition tend to discount periods when many fish are mobile (e.g., spawning migrations or fry dispersal), all of which can obscure a comprehensive understanding of fish movements (Börger et al. 2008). Although case studies that attempted to address some of these concerns found that life-long movements of stream salmonids were relatively restricted (Heggenes et al. 1991; Lobón-Cerviá 2000; Hutchings and Gerber 2002), the fish under evaluation occupied small streams with barriers to movement that might discourage mobility as a life history strategy (Fausch et al. 2002). In larger, more connected stream networks, the movements of salmonids during some life history phases have been frequent and substantial (Schmetterling 2001; Zurstadt and Stephan 2004; Colyer et al. 2005), although habitat-size-related patterns in movement remain poorly understood (Woolnough et al. 2009).

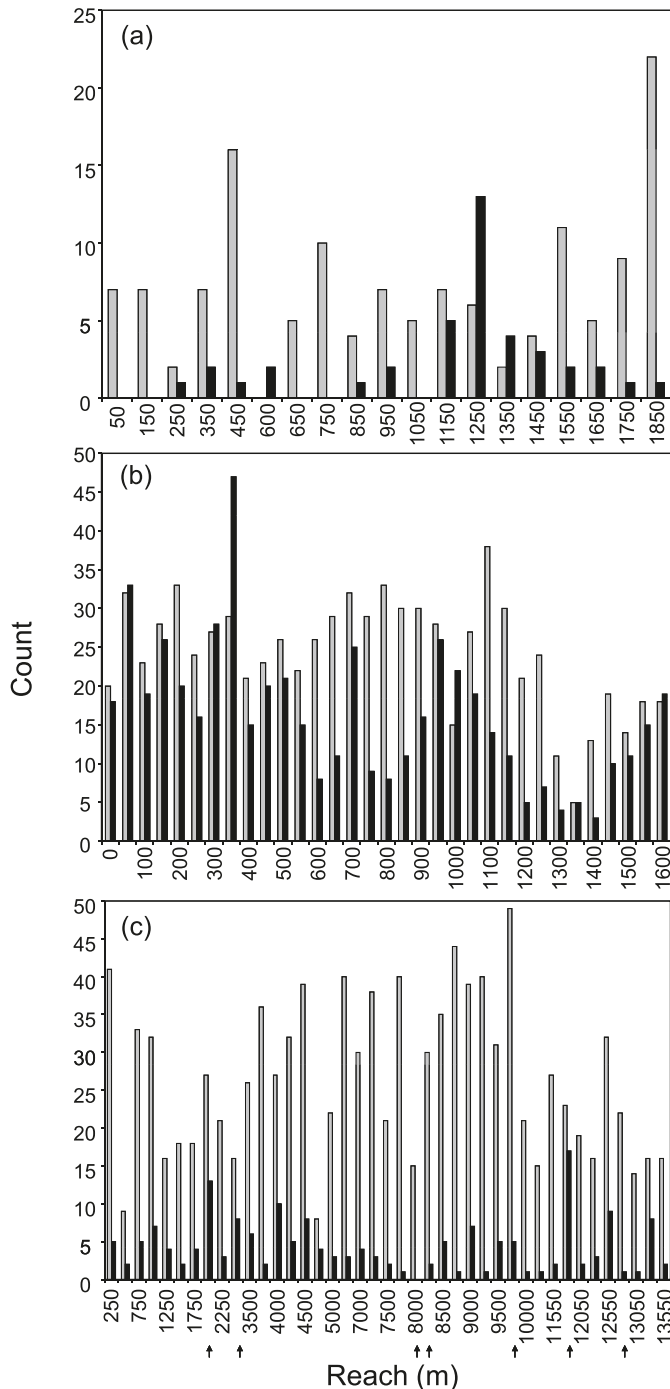
The goal of this paper is to assess the medium- and large-scale movements of individuals and age groups of Colorado River cutthroat trout (*Oncorhynchus clarkii pleuriticus*) using a variety of methods over the course of a generation (5–6 years) in a stream network with segments of different length and connectivity to the main stem. Specifically, the objectives are to determine whether fish characteristics, location, and length of observation are related to the prevalence, extent, and direction of movement. In light of these results, I revisit notions about the mobility of stream fishes.

Materials and methods

Study area

The North Fork Little Snake River watershed is in south-central Wyoming, USA. This study was conducted in a 39.7 km stream network (above a weir blocking fish migration) composed of 16 stream segments: the main-stem North Fork Little Snake River below (mean width 5.4 m) and above (mean width 2.2 m) a water diversion; six tributaries entirely below diversions (or lacking them; mean width 0.6–2.2 m);

Fig. 2. Distribution of captures of age-1 (black bars) and age-2 and older (grey bars) Colorado River cutthroat trout in (a) upper Ted Creek, (b) Rose Creek, and (c) the North Fork Little Snake River main stem below the water diversion. Arrows on panel (c) denote approximate locations of the mouths of fish-bearing tributaries. Note that reach spacing on the x axis on this panel is not consistent.



and four tributaries with portions below and above water diversions (mean width 1.4–3.2 m; Fig. 1). These cold (mean August water temperature 8.9–12.5 °C), high-elevation (mouths at 2250–2770 m) streams had snowmelt-dominated flows that peaked in May or June. Cutthroat trout spawned from late May to early July, and fry emerged from August to

September. The short growing season produced slow-growing fish that rarely exceeded 250 mm total length.

A variety of features probably influenced the connectivity and extent of fish populations. During high flows, the screened diversion structures passed a portion of the flow into an underground pipe; the remainder of the flow returned to each channel via a smooth, steep bypass pipe that either spilled onto rubble–boulder riprap before collecting 10–20 m downhill in a constructed pool or emptied directly into such a pool. Movement was considered more likely at the latter sites (Ted Creek and the upper North Fork Little Snake River). The upstream extent of fish terminated abruptly at or near the base of water diversions in two segments and at waterfalls or headcuts in four segments and gradually diminished in three other segments. Cascades exceeding gradients of 20%, generally containing vertical steps over 1 m, were also present in several tributary segments.

Sampling

I measured thalweg length of each stream with a drag tape, flagged and staked the channels at 50 m intervals, and visually noted whether fish were present. The upstream extent of cutthroat trout was later confirmed by electrofishing near and upstream from where they were last observed in each segment (Young et al. 2005).

Several methods were used to capture cutthroat trout. From 1996 to 1999, crews electrofished essentially the same set of 25 m reaches ($n = 245$) distributed at systematic intervals throughout the watershed (see Young et al. 2005 for additional details). Intervals between electrofishing reaches varied from 50 to 250 m to ensure an adequate number of samples in all streams to estimate fish abundance and resulted in sampling 10%–45% of each stream. From 1997 to 1999, crews electrofished Rose Creek in its entirety, save the uppermost 200 m, which was in Colorado and contained few fish. In 2000, crews electrofished all pools in the basin except in the lower 11 km of the main stem, and in 2001 they electrofished only pools in the lower and upper main stem and in tributaries downstream from water diversions. All electrofishing was conducted during low flows from mid-July to late August. Insufficient labor was available to electrofish the entire watershed in any year, thus crews also angled throughout most of the basin from 1997 to 2001 and deployed minnow traps (or hoop nets without leads) for 1–2 weeks in portions of almost all segments in 1997 and 1998. These methods were used primarily in non-electrofishing reaches because it was assumed that electrofishing would be more efficient than these other methods in the annually sampled reaches.

All cutthroat trout captured were measured (total length in millimetres and mass in grams) and checked for tags. From 1996 to 1998, fish ≥ 80 mm received a passive integrated transponder tag. Fish obtained by electrofishing were released within 25 m of their capture location, and those taken by other methods were released at the site where captured.

Three events may have altered positions of cutthroat trout in this basin during the study. First, during 25–27 August 1997, managers attempting to eradicate brook trout by electrofishing collected large numbers of Colorado River cutthroat trout in the North Fork Little Snake River main stem from the weir to the mouth of Harrison Creek. These fish

Fig. 3. Length–frequency distribution of Colorado River cutthroat trout in the North Fork Little Snake River main stem below the diversion (grey bars) and the below-diversion segments of its tributaries (including all of Rose Creek; black bars).

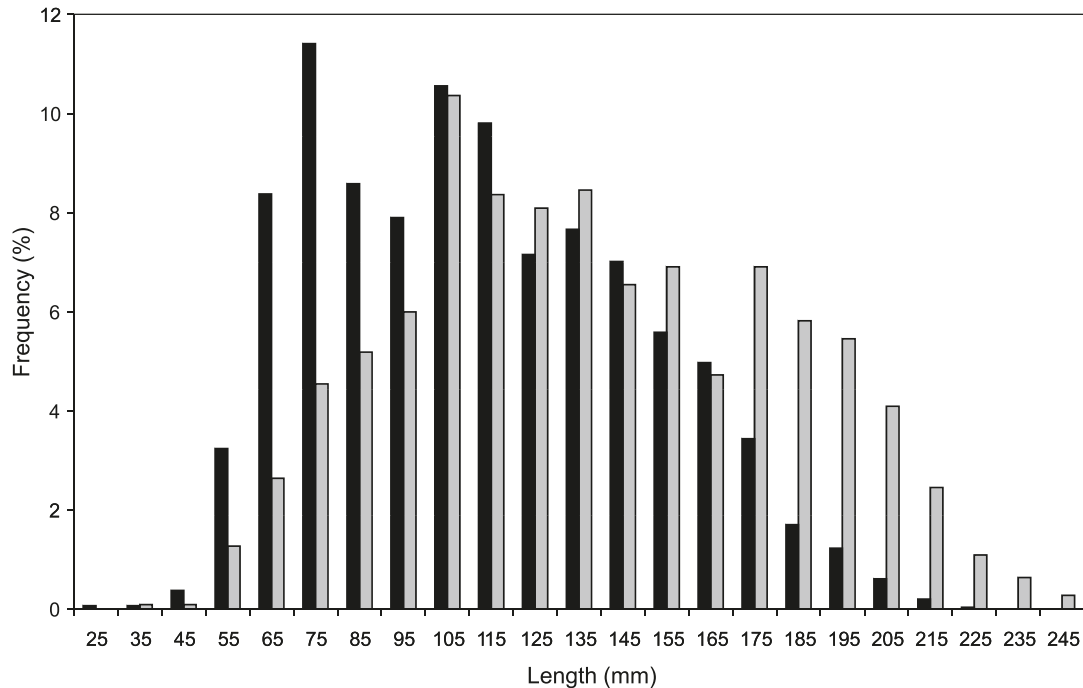


Table 1. Frequencies (% in parentheses) of fish that occupied a single site or were mobile relative to the number of years between first and last capture.

Movement class	Years between first and last capture				
	0	1	2	3	4
Single site	115 (64)	192 (61)	79 (61)	32 (46)	5 (36)
Mobile	65 (36)	125 (39)	50 (39)	38 (54)	9 ^a (64)

^aIncludes two fish captured 5 years apart.

Table 2. Direction (% in parentheses) and median distance (maximum in parentheses) of movement by tagged Colorado River cutthroat trout originating from the main stem or the tributaries.

Segment	Direction moved (number of fish)			Distance moved (m)		
	Upstream	Downstream	Complex	Upstream	Downstream	Complex
Main stem	110 (64)	40 (23)	23 (13)	400 (9020)	250 (5100)	895 (7520)
Tributaries	53 (46)	38 (33)	23 (20)	175 (1150)	123 (6580)	470 (2075)

Note: Complex movements were defined as a combination of upstream and downstream movements within a single segment or movement down one segment and up another.

were held in live cars distributed at roughly 0.5–1.0 km intervals, which led to the displacement of many individuals and the mortality of 42 marked fish and 373 others. This displacement, however, was after all fish sampling in the main stem that year. Second, on 31 July and 1 August 1999, a debris torrent rerouted portions of the uppermost 600 m of the North Fork Little Snake River main stem above the water diversion. Crews did not locate any fish in this reach in subsequent sampling. Third, the 1995 year class of Colorado River cutthroat trout in this basin was very small (M.K. Young, unpublished data). The near-absence of this year class may have affected size-related patterns in mobility (primarily through sample size alteration).

Analyses

Length–frequency

Length–frequency analyses were used to compare movement patterns of fish too small to tag with those of larger tagged fish. I examined spatial variation in the abundance of fish of different ages by using the Kuiper two-sample test to compare counts of presumptively juvenile (age-1) and adult (age-2 and older) fish in each stream segment by reach. The analysis was based on the pooled data from the 1996–1999 repeat electrofishing reaches. Because sampling was conducted each year before fry emergence, the youngest fish captured were age 1. Length–frequency bar graphs were

used to identify juvenile and adult age classes in each stream segment. Although large variation in site-specific survival is possible, I interpreted significant spatial differences in relative abundance of these two age classes as evidence of the postjuvenile redistribution of fish (Newman and Waters 1989; Schlosser and Angermeier 1995; Petty et al. 2005).

To assess fish age at the time of redistribution, I compared the length–frequency bar graphs of fish in the lower main-stem North Fork Little Snake River with those in tributary segments below or lacking water diversions. Previous research (Jespersen 1981; Young 1996) demonstrated that adult cutthroat trout made spawning runs into the tributaries and that relatively little spawning habitat was present in the main stem. Moreover, few age-1 fish were present in the main stem despite it containing the highest densities of Colorado River cutthroat trout in this basin (Young et al. 2005). Thus, I interpreted the modal length in the length–frequency bar graph for the lower North Fork Little Snake River as indicative of the size (and thus age) by which juvenile fishes in the tributaries had migrated to the main stem (Solomon and Templeton 1976; Moring et al. 1986).

Mark–recapture

These analyses required a biologically defensible standard for mobility (cf. Larson et al. 2002; Holyoak et al. 2008), for which I used summer–autumn home range size (Crook 2004). Because median summer home range for adult Colorado River cutthroat trout in this basin was 32–45 m, median autumn home range was 38 m, and no position shift was observed between seasons (Young 1996, 1998; also see Hilderbrand and Kershner 2000), I deemed fish occupying positions >50 m apart as mobile fish. Therefore, I regarded fish captured and recaptured (1996–2001) in only one 50 m reach, or in that and an adjacent 50 m reach, as exhibiting site fidelity (single-site fish), whereas those occupying positions farther apart were considered mobile. Distance moved was considered the distance between the midpoints of the upstream-most and downstream-most 50 m reaches in which a fish was captured. For fish that also moved from the main stem to a tributary, distance moved also included the distance from the tributary mouth to the midpoint of the occupied tributary reach.

Preliminary analyses indicated that capture method, but not fish length or location, affected the probability of recapture (M.K. Young, unpublished data). Because of this and the variation in annual effort and environmental and anthropogenic disturbances affecting portions of the watershed, I could not develop an overall model to assess movement. Thus, I divided the remaining analyses into two groups based on (i) probability of movement and (ii) distance and direction moved.

Movement probability

I used logistic regression to assess whether length at first capture, number of captures, and days between first and last capture were related to the probability of fish being mobile. Because the last comparison provided a statistically significant but poorly fitted model, the analysis was repeated by pooling all captures within each year and using a Cochran–Armitage trend test to compare the proportions of recaptured

fish that were mobile with the years between first and last capture.

To address the effects of location on probability of movement, I used χ^2 tests to compare the proportions of mobile and single-site fish between locations. Based on their site of first capture, I considered fish as originating from the main-stem North Fork Little Snake River above the weir or the tributaries.

To determine whether fish condition was related to mobility, I used an analysis of covariance of the log–log relation between length and mass, with site fidelity as the classification variable (Gowan and Fausch 1996a; Hilderbrand and Kershner 2004). Because their length–mass regressions were similar and their sample sizes large, fish from Rose Creek and the lower North Fork Little Snake River main stem were used. These analyses were run only on fish captured in consecutive years, but examined in two ways: (i) the condition of mobile and single-site fish in the year before mobile fish moved and (ii) the condition of both groups in the following year. Analyses were done for each year separately because the year $\times$ length effect was significant in both models and these years provided sufficient sample sizes. The same approach was also used to calculate specific growth rates (Kahler et al. 2001) of mobile and single-site fish for 1996–1997, 1997–1998, and 1998–1999 in these two segments, with length as the covariate.

Movement extent and direction

Maximum distances between occupied positions of mobile fish were nonnormally distributed, thus I used rank correlation to relate length at first capture, number of captures, and days between first and last capture to maximum distances. The effect of location on maximum distance moved was evaluated with respect to direction of travel. Direction was based on the order of captures and classified as upstream, downstream, or complex; the latter was defined as a combination of upstream and downstream movements within a single segment or movement down one segment and up another. Differences in the proportions of each direction class within and between locations were evaluated using χ^2 tests. Differences in the maximum distances between occupied positions for each direction class within a location were examined by using Kruskal–Wallis tests, and pairwise comparisons within a direction class but between locations were performed using Bonferroni-corrected Wilcoxon two-sample tests. Finally, I described the range in recapture sites of fish originally marked in each segment.

Results

Length–frequency

The distribution of juvenile fish tended to differ from that of older individuals at the scale of reaches within stream segments. In nearly half of the segments — the lower North Fork Little Snake River and Solomon, Rose, Green Timber, Rhodine, upper Third, and upper Ted creeks — there was a significant difference between the distributions of age-1 and of older fish ($P < 0.001$ – 0.043 ; Fig. 2). Juvenile fish less than 105 mm long were underrepresented in the main stem relative to their abundance in below-diversion tributary segments (Fig. 3). Length–frequencies indicated that most tribu-

Table 3. Matrix of the stream segments where tagged cutthroat trout were captured and recaptured from 1996 to 2001.

Segment of recapture	Segment of origin												
	NF-l	Solo	Rose	Har-l	Har-u	GT	Dea-l	Dea-u	Thi-l	Thi-u	Ted-l	Ted-u	NF-u
NFLS (lower)	310		2	4		5	6		14		4		6
Solomon		29											
Rose	3		111										
Harrison (lower)	3			27									
Harrison (upper)					7								
Green Timber	5					67	29	2					
Deadman (lower)	4												
Deadman (upper)								7					
Third (lower)	5								25				1
Third (upper)										3			
Ted (lower)	6										2	2	1
Ted (upper)												3	
NFLS (upper)	3												22
Rhodine	1												4
Spawn													1
Happy													2
Total recaptured	340	29	113	31	7	72	35	9	39	3	6	5	37
Total tagged	1720	293	420	217	41	354	189	51	89	29	48	45	200

Note: NFLS and NF, North Fork Little Snake River; Solo, Solomon; Har, Harrison; GT, Green Timber; Dea, Deadman; Thi, Third; Rhod, Rhodine; Spaw, Spawn; Happ, Happy; l, lower; and u, upper. The total of recaptured fish from the lower North Fork Little Snake River and Spawn Creek were increased by one to account for fish that were captured in three different segments.

tary fish did not reach this length until age 2, implying that there was a widespread redistribution of this and younger age classes to the main stem. Adults in the main stem also tended to attain larger sizes than those in tributaries.

Mark-recapture

Over the 1833-day marking and recapture phase, there were 4607 captures: 2998 captures of fish captured once and 1609 captures of 710 fish captured two to six times. Of the latter, 287 fish occupied positions greater than 50 m apart.

Movement probability

The probability of being mobile was unrelated to length at first capture ($P = 0.65$) and to number of captures ($P = 0.43$). Mobility was significantly related to the number of days between first and last capture (intercept = -0.655 , $\beta = 0.0006$, $n = 710$, $P = 0.005$), but with a poor fit (Hosmer–Lemeshow goodness-of-fit test, $\chi^2 = 22.16$, $df = 8$, $P = 0.0046$). Nevertheless, there was an increasing trend between the proportion of recaptured fish that were mobile and the number of years between first and last capture (one-sided Cochran–Armitage test, $z = -2.72$, $P = 0.003$; Table 1). A greater proportion of fish first marked in the main stem were mobile than were fish first marked in a tributary (0.48 vs. 0.33, $\chi^2 = 16.65$, $df = 1$, $P < 0.0001$).

For fish from the lower main-stem North Fork Little Snake River and Rose Creek, there were no differences in the length–mass regressions of mobile and single-site fish in the year that mobile fish moved ($n = 42$ –117; main effect of movement, $P = 0.27$ –0.59; length $\times$ movement interaction, $P = 0.26$ –0.54) or in the subsequent year ($n = 42$ –117; main effect of movement, $P = 0.17$ –0.66; length $\times$ movement interaction, $P = 0.18$ –0.64). Specific growth rates of mobile fish tended to be greater than those of single-site fish (main effect of movement: 1996, $n = 42$, $P = 0.12$; 1997, $n = 117$, $P = 0.50$; 1998, $n = 70$, $P = 0.0395$; combined comparison of probabilities, $\chi^2 = 12.09$, $df = 6$, $P = 0.063$). The length $\times$ movement interaction was not significant in any year ($P = 0.11$ –0.59).

Movement extent and direction

The distance moved by mobile fish was not related to the number of captures (rank correlation, $P = 0.76$) or days between first and last capture ($P = 0.94$). Distance was, however, related to length at first capture (Spearman's correlation coefficient = 0.136, $n = 285$, $P = 0.02$). Regardless of location, mobile fish tended to move upstream more than downstream or in complex ways (main stem, $\chi^2 = 73.75$, $df = 2$, $P < 0.0001$; tributaries, $\chi^2 = 11.84$, $P = 0.0027$), and main-stem fish had a greater tendency to move upstream and a lesser tendency to move downstream or in complex directions than did tributary fish ($\chi^2 = 8.20$, $df = 2$, $P = 0.017$; Table 2). Distances traveled upstream and downstream were greater for fish first captured in the main stem than for those in the tributaries (upstream, $z = -4.51$, $P < 0.0001$; downstream, $z = -3.22$, $P = 0.001$), but the length of complex movements did not differ ($z = 1.17$, $P = 0.24$). Within the main stem and the tributaries, there were differences in the distances moved with respect to direction class (main stem, Kruskal–Wallis $\chi^2 = 9.26$, $df = 2$, $P = 0.01$; tributaries, Kruskal–Wallis $\chi^2 = 16.71$, $df = 2$, $P =$

0.0002). In the main stem, complex movement distances were marginally longer than those associated with upstream movements ($z = 1.65$, $P = 0.098$), and both were longer than those associated with downstream movements (complex, $z = 2.46$, $P = 0.0137$; upstream, $z = -2.40$, $P = 0.0163$). In the tributaries, complex movements were greater than upstream ($z = 3.17$, $P = 0.0015$) and downstream ($z = 3.68$, $P = 0.0002$) movements, whereas the latter two did not differ ($z = -1.85$, $P = 0.065$).

Overall, 87% of tagged fish remained within the stream segment where they were captured (Table 3). Fish moved between the North Fork Little Snake River main stem and most tributary segments that lacked or were below diversions (except Solomon Creek). Overlap in main-stem locations among fish that used different tributaries was common (Fig. 1). Fish that used both the main stem and a tributary tended to travel more extensively in the main stem (median maximum distance 1450 m, range 30–8320 m) than in the tributary (median maximum distance 150 m, range 0–1000 m, $n = 9$ tributary segments).

Discussion

Over the course of their lives, a substantial proportion of the cutthroat trout in this network of small streams undertook wide-ranging and complex movements that appeared to be influenced by a suite of variables. These movements began with young fish, as indicated by the differing distributions of juveniles and adults in most stream segments. Age-structured spatial distributions have been previously observed in populations of trout (Moring et al. 1986; Young and Guenther-Gloss 2004; White and Rahel 2008) and other stream-dwelling fishes (Schlosser and Kallemeyn 2000). The distribution of salmonid fry in lotic environments generally mirrors that of spawning locations (Bozek and Rahel 1991; Steingrímsson and Grant 2003; Einum and Nislow 2005), which are patchily distributed in turbulent mountain streams because of limitations in gravel supply or the appropriate channel configuration (Magee et al. 1996; Moir et al. 1998; Baxter and Hauer 2000). The eventual redistribution of older juveniles (Milner et al. 1979; Moring et al. 1986; Petty et al. 2005) may be attributable to changing habitat requirements (Everest and Chapman 1972; Morantz et al. 1987) or to intra-cohort competition for sites providing adequate foraging opportunities (Chapman 1962; Elliott 1994).

Movement rates of stream fishes have been associated with growth rates (Kahler et al. 2001; Steingrímsson and Grant 2003), condition (Gowan and Fausch 1996a, 1996b; Hilderbrand and Kershner 2004), and length (Fraser et al. 2001; Gresswell and Hendricks 2007). The observations that movement was somewhat more likely among rapidly growing cutthroat trout and that the largest mobile fish tended to move the farthest are consistent with these earlier findings. The absence of a relation between fish size and the probability of movement is not, but this may be attributable to the role of dominance in spatially structuring salmonid populations. As fish grow or energy demands increase, the number of sites that provide net bioenergetic gains within many streams decreases (Rincón and Lobón-Cerviá 2002), necessitating more distant movements (Railsback et al. 1999). In addition, the largest individuals in many populations of drift-feeding salmonids

appear to be among the first individuals to move (Railsback and Harvey 2001; Gowan 2007), presumably because of discrepancies between their greater bioenergetic demands and drift rates at foraging sites (Jonsson and Jonsson 1993). If large fish displace less behaviorally dominant individuals from the most energetically favorable sites (Hughes 1992; Gowan and Fausch 2002), the result would be a cascade of movements among fish of all sizes that could obscure length-related patterns in the likelihood of movement (Railsback and Harvey 2002). This argument is supported by the observation that the longer a fish was observed, the more likely it was to move in this study and others (Gresswell and Hendricks 2007; Roberts and Angermeier 2007). Regardless, there is ample support to suggest that food availability, and more generally habitat productivity, affect the prevalence of local movements and large-scale migrations in stream fishes (Olsson et al. 2006).

The tendency to move and the distance traveled were greater for fish first marked in the main stem than those in the tributaries. In part this could be a response to the quantity of habitat in which to move (Crook 2004), although fish in tributary segments below diversions had access to as much habitat as fish occupying the main stem. A more plausible explanation is that tributary fish preferentially exhibited greater site fidelity or, when mobile, tended to move shorter distances (Letcher et al. 2007). The dichotomy in movement and adult size between the main stem and tributaries is analogous to that in larger basins in which more productive, lower-elevation waters harbor large migratory adults that co-occur (as juveniles and during spawning) in smaller, less productive tributaries with smaller fish exhibiting resident life histories (Jonsson and Jonsson 1993). The interplay between juvenile metabolic rates and natal habitat productivity may generate these patterns. In cold, unproductive tributaries, juveniles with low metabolic rates are more likely to become residents, whereas faster-growing fish are more likely to migrate (Forseth et al. 1999; Morinville and Rasmussen 2003). In contrast, where high productivity permits rapid growth rates of juvenile salmonids, resident life histories may have higher fitness (Morinville and Rasmussen 2003; Olsson et al. 2006). This may explain why no fish were observed moving between Solomon Creek, the warmest tributary with the highest fish densities and second-highest average condition (M.K. Young, unpublished data), and the main stem.

Gross (1987) argued that migration is a trade-off between the increased age-specific fecundity obtained in more productive environments and the greater metabolic requirements and mortality rates associated with moving. In this stream network, the trade-off may only be favorable for individuals that originated from the lowermost portions of tributary streams (Bohlin et al. 2001). Fish that left tributaries often traveled extensively within the main stem — up to several kilometres — whereas fish leaving the main stem to enter tributaries rarely penetrated more than a few hundred metres. It is also likely that cascades and waterfalls in many tributaries slowed or blocked upstream movements (Kahler et al. 2001), and most water diversions impeded or prevented movement in both directions.

The patterns in movement direction over time are more difficult to interpret. Observations of more prevalent and longer movements upstream across years by subadult and adult

stream fishes are not without precedent (Gowan and Fausch 1996a; Skalski and Gilliam 2000; Roberts and Angermeier 2007). The most parsimonious explanation is that these movements compensate for the downstream drift of most fry (Hall 1972), which seemed to be evident here. If so, many fish are occupying locations they visited after leaving natal sites, with a tendency to occupy positions closer to natal areas with time. In addition, many movement tracks involved combinations of upstream and downstream shifts. That some fish migrate downstream before moving upstream, between a tributary and the main stem or vice versa, is uncommon but has been documented for adults in this basin (Young 1996) and elsewhere (Brown and Mackay 1995; Schmetterling 2001; Hogen and Scarnecchia 2006) and for juveniles (Solomon and Templeton 1976; Newman and Waters 1989; Webb et al. 2001). Overall, this diversity in directionality may indicate substantial complexity in the motivation for and outcome of fish movements (Fausch 2010), and I echo the call of Skalski and Gilliam (2000) that more attention be directed to this aspect of the movement ecology of aquatic organisms.

Generalizing about movements by stream fishes continues to be a thorny issue. Methodological problems inherent to mark–recapture studies remain difficult to overcome, such as the differential detectability of mobile and stationary fish (Gowan and Fausch 1996a) or failure to sample fish moving to distant portions of a stream network (Albanese et al. 2003). The present study was no exception. The probability of detecting tagged fish was greatest with electrofishing, and because the same reaches (about 15% of the watershed) were electrofished annually from 1996 to 1999, the probability of detecting fish that failed to move was higher than the probability of detecting fish that exited these reaches. In addition, although sampling was done in all contiguous portions of the watershed, I could not account for downstream movements of individuals over the weir on the lower main stem or for individuals that entered the water collection system. In addition, fish movements have been linked to environmental events (e.g., floods or droughts; Harvey et al. 1999; Steingrímsson and Grant 2003; Albanese et al. 2004) that were unlikely to be detected in the present study. Taken as a whole, these factors probably led to underestimating the extent and prevalence of lifetime movements of cutthroat trout in this watershed.

It has been argued that limited mobility is the norm among salmonids in streams (Rodríguez 2002), and in this study most recaptured fish were found in the same segment, and often the same reach, where originally captured. Yet additional evidence from this study — the differences in the distribution of juvenile and adult fish and generation-long observations of movement of tagged individuals in all stream segments and between many of them — coupled with previous observations of radio-tagged fish (Young 1996, 1998; Young et al. 1997), support the conclusion that Colorado River cutthroat trout in this drainage alter their positions on diel, seasonal, and annual cycles to feed, grow, reproduce, and seek refuge from unfavorable environments. None of the patterns of movement described here are unique to this watershed or to cutthroat trout in streams (Harvey 1998; Waples et al. 2001; Schrank and Rahel 2004). Rather, they are concordant with other observations of stream fishes in patchy environments in which movements between complementary habitats enable populations to persist (Schlosser and Angermeier

1995). Nonetheless, there may be little consistency among stream fishes (or other aquatic organisms; Downes and Keough 1998) with regard to the frequency and extent of nonmigratory and migratory movements (Northcote 1992, 1997). Different patterns of movement of stream fishes probably reflect local variation in habitat quality, population and community structure, and life history strategies. Climatic variation or watershed disturbances that alter food availability, potential growth, or habitat connectivity may alternately favor and discourage movements and heighten this complexity. Given the spatial variability in productivity and network structure typical of river basins (Thorp et al. 2006), variation in movement tactics attributable to environmental heterogeneity might be the norm even within a relatively small watershed (Cucherousset et al. 2005; Campbell Grant et al. 2007).

In conclusion, much emphasis has been placed on the restricted movement or pervasive mobility characteristic of fish of particular ages, during certain seasons, or in particular environments. The greater challenge, however, is to consider fish populations from a whole-basin and generation-long perspective (Hughes 2000; Fausch et al. 2002; Roberts and Angermeier 2007). In this view, movement will be recognized as a continuum of varying prevalence, duration, and extent in spatially and temporally heterogeneous stream networks.

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