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Seasonal migrations of adult and sub-adult redband trout in a high desert basin of Eastern Oregon, USA

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Abstract – Redband trout (*Oncorhynchus mykiss gairdneri*) migrations were tracked between March 2007 and June 2009 in the Donner und Blitzen River, Oregon, USA, using radio telemetry and PIT tags. We investigated the upstream extent and timing of spawning migrations for two groups of trout, considered the factors that influenced the rate of trout migration and explored the seasonal patterns of redband trout migration related to temperature and flow conditions. We found that trout made long-distance migrations (up to 91 km) to spawn. Spawning trout from the lower river and middle river migrated to the same reaches, but lower river trout reached spawning habitats later than individuals from the middle river. Migration rate had a positive relationship with fork length and mean river discharge. We also found that redband trout made upstream spring migrations as sub-adults and as adults. Whereas adult trout migrated to spawn, immature individuals migrated to river segments with more favourable thermal conditions. In both cases, migrations occurred where seasonally appropriate or life-stage-specific habitat patches for growth, survival, or reproduction were spatially segregated.

Key words: migration; temperature; PIT; salmonid; redband trout; telemetry

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Introduction

Migrations are common in salmonids and are indicative of heterogeneous and spatially separated habitats that allow fish to optimise growth, survival, and reproduction (Northcote 1997). Salmonids exhibit a wide variety of migratory behaviours (Baxter 2002; Meka et al. 2003; Mellina et al. 2005), which are best understood in the context of landscape-scale distribution of habitat patches and refugia from harsh environmental conditions or risk of predation (Schlosser 1995; Gresswell et al. 1997). Diversification of migratory life histories allows a population to exploit various habitats, which may increase both its productivity and its resilience under changing conditions (Rieman & Dunham 2000).

Although migrations can provide many benefits to stream salmonids, they are not without risks and costs. Salmonids that are unable to return to their spawning habitats at the correct time may fail to reproduce (Caudill et al. 2007). Migrations are energetically costly (Rand & Hinch 1998), and transitional habitats may be unproductive or increase the risk of predation. Stream impoundments, even those with fish passage facilities, can exacerbate these problems by delaying fish migrations (Caudill et al. 2007). Because of these costs and risks, time in transit may influence growth and survival rates for stream fishes moving between habitat patches (Schlosser 1995).

Redband trout (*Oncorhynchus mykiss gairdneri*) is an archaic subspecies in the coastal rainbow trout lineage (Behnke 1992). The Donner und Blitzen (Blitzen) River has the largest migratory population of redband trout in the Great Basin region of the Western United States (Bowers et al. 1999; Dambacher et al. 2001). In the Steens Mountain Cooperative Management and Protection Act (2000), the 106th U.S. Congress designated parts of the Blitzen River as the nation's first trout reserve and stated that it would be managed 'in a manner that conserves the unique population of redband trout native to the Donner und Blitzen River.' Despite national recognition of the value of Blitzen redband trout, little is known about the migratory life history or landscape-scale habitat usage of the population. Although historical data on the abundance of redband trout in the Blitzen River is limited, anecdotal accounts indicate that the population, particularly the migratory component, has declined over the last century (Hosford & Pribyl 1983).

The objectives of this study were to examine the migratory behaviour of Blitzen River redband trout to better understand the factors related to the timing, rate and magnitude of the migration. The extreme fluctuation between summer high (28.6 °C) and winter low (0 °C) temperatures and the diversity of habitats in the Blitzen River provided a unique opportunity to study the way that trout use migration to adapt to local conditions. We used the definition of migration from Northcote (1997): a distinctive type of large-scale movement that is repeated at regular periods during the lifespan of an individual, involves a large fraction of the population, and often implies returning to natal habitats for reproduction. This study explored the landscape-scale migration patterns of redband trout in the Blitzen River by addressing three questions: (i) Do sexually mature trout that reside in different sections of the river prior to migration have different spatial and temporal spawning patterns? (ii) Is trout migration rate influenced by fish size (fork length), stream temperature, river discharge, number of dams passed, or fish tagging method? and (iii) Are trout migrations related to seasonal changes in stream temperature conditions?

Methods

Study location

This study was conducted in the Donner und Blitzen River, which is located in the high desert region of south-eastern Oregon (Fig. 1). The Blitzen River drains into Malheur Lake and has no further outlet to the ocean. This basin has an area of 2045 km^2 and a drainage density of 0.33 $km \cdot km^{-2}$. Its elevation ranges from 1248 m at Malheur Lake to 2967 m at the top of Steens Mountain. The Blitzen River mainstem is 128 km long. The tributaries, most of which drain the west slope of Steens Mountain, flow through deep, glacially carved valleys of basalt and andesite bedrock and have a parallel drainage pattern. Major tributaries included in the study were Indian, Fish, and Bridge Creeks and the Little Blitzen River (Fig. 1). Mean annual precipitation in the basin ranges from less than 40 cm at lower elevations to over 100 cm at the higher mountain elevations (Taylor 2009). Most precipitation falls as snow during winter months and most run-off occurs as snow melt during spring.

For the purposes of this study, we divided the Blitzen River into three sections, lower river, middle river, and upper river, based on differences in stream morphology. The lower river includes the area from the mouth of the Blitzen River (rkm 0) to the confluence with Bridge Creek (rkm 67). This stream section consists of a low-gradient and highly sinuous channel, except where artificially straightened, with a predominantly sand and silt bedload. Because there is little gravel in this section, it is not likely that it provides trout spawning habitat. The middle river extends from Bridge Creek up to the Page Springs Weir (rkm 79). The middle river is characterised by a low-gradient, unconstrained channel with pool-riffle habitat and gravel as the primary substrate type. The upper river, above the Page Spring Weir, is constrained by steep canyon walls and is characterised by boulder-strewn rapids interspersed with pockets of gravel.

The Malheur National Wildlife Refuge (MNWR) has four primary diversion dams on the Blitzen River that are operated during the spring snowmelt period to maintain wetland habitat for breeding waterfowl. Three of those dams (Sodhouse, rkm 6, Busse, rkm 35, and Grain Camp, rkm 48) are located in the lower river, and the fourth (Page, rkm 76) is located in the middle river (Fig. 1). Sodhouse, Busse, and Page dams have Denil fish ladders, a type of ladder with closely spaced baffles that create low-flow velocities which facilitate upstream movement of fish, and Grain Camp dam has a pool-weir fish ladder.

Environmental conditions

Stream discharge and temperatures were monitored over the course of the study. The U.S. Geological Survey collected river discharge data at 15-min intervals at the Page Springs Weir gauging station, located immediately upstream of the Malheur National Wildlife Refuge boundary. Water temperature was recorded at 30-min intervals at 10 locations on the Blitzen River with Hobo (Onset Computer Corporation, Bourne, MA, USA) temperature loggers. In the year 2007, one temperature logger was damaged and one was exposed to air, while in 2008, one temperature logger was exposed to air; therefore, data recorded by these units were not included in any of the analyses. We summarised stream temperatures for both summer and winter conditions. For summer high temperatures, a 7-day moving mean was calculated from the daily maximum temperature. The highest of those 7-day means (7-day max. mean) was used to characterise the hottest period at each monitoring location.

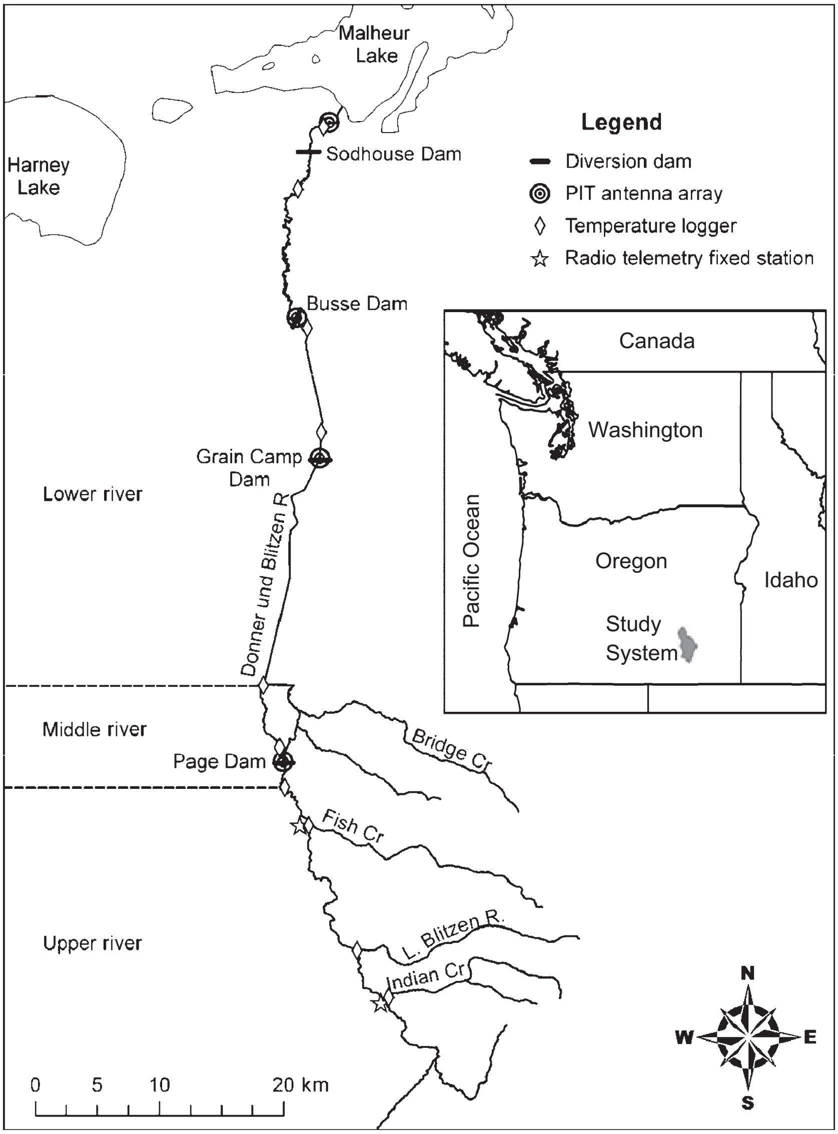

Fig. 1. Map of the Blitzen River illustrating the locations of diversion dams, passive integrated transponder tag readers, temperature loggers, and radio telemetry fixed stations.

Fish tagging and scale analysis

Redband trout were caught in fish traps located at the upstream end of fish ladders at Sodhouse (rkm 6), Busse (rkm 35), and Page (rkm 76) dams and by angling near the dams. Traps were set and checked daily 4–7 days a week from late March to early June of 2007 to 2009. Angling with artificial lures was employed approximately 5 h per week below the dams in April and May each year. Additionally, trout were sampled by angling above the dams on isolated occasions in 2007 and 2009 and for a concerted 3-day effort in late March 2008. On one occasion in 2007, we opportunistically netted fish from the Grain Camp fish ladder (rkm 48). Because our sampling techniques targeted fish that were moving in the spring, our scope of inference in this study was limited to migratory individuals. Each captured trout was measured (fork length to the nearest mm) and weighed (to the nearest g). We took scales from a subset of the trout captured. Although fish were not sampled randomly, we attempted to take scales from trout across the range of sizes to fully represent the population. Sexual maturity was assessed for radio-tagged fish based on external characteristics and by examining gonads during the tagging surgery. Trout sex was recorded for mature individuals.

We tagged trout with radio transmitters and passive integrated transponder (PIT) tags. We used radio transmitters to learn how far upstream in the river fish migrated. Radio transmitters had the advantage of a high redetection rate and the ability to track fish throughout the river. Radio tagging was limited, however, by transmitter size, cost and our desire not to impact every fish in the population with such an invasive tagging procedure. We had a limited number of radio transmitters, and we deployed them throughout the migration season rather than only tagging the fish caught during the first few days of sampling. We used three models of transmitters manufactured by Lotek Wireless Inc., Ontario, Canada, including MCFT-3A (16 g), MCFT-3FM (11 g), and NTC-6-2 (4.5 g). PIT tags (Texas Instruments, Dallas, TX, USA) were used to track multi-year migrations and fish migration rates, and because they are smaller, less invasive, and less expensive. PIT tags (23 mm in length and 1 g in weight) were used to tag all trout over 100 mm fork length.

Radio transmitters were surgically implanted in the peritoneal cavity, and PIT tags were inserted into the body cavity of smaller trout (FL < 300 mm) and the dorsal sinus of larger trout (FL ≥ 300 mm). All surgeries were conducted on site at the capture location. Trout were anesthetised in an aerated holding tank with approximately 100 $mg \cdot l^{-1}$ tricane methanesulphonate (MS-222) solution with 120 $mg \cdot l^{-1}$ of bicarbonate buffer. Anaesthesia typically occurred in 2–4 min. For the surgery, trout were placed ventral side up in a wet, foam cradle. The gills of the fish were irrigated with anaesthetic solution and stream water during the surgery. A 1.5- to 2.5-cm-long incision, just wide enough to accommodate the transmitter, was made on the fish anterior to the pelvic girdle of the fish, offset 2 cm from the mid-ventral line. A cannula shielded with plastic tubing was used to guide the transmitter antenna to the exit location posterior to the pelvic fin (Ross & Kleiner 1982). After placing the transmitter in the body cavity, the incision was closed with 2–3 sutures of monofilament absorbable material with a simple interrupted 3-2-1 surgical pattern (Wagner et al. 2000). All surgical equipment was disinfected between uses. Trout were allowed to recover in a covered tank with stream water for at least 15 min and until they were fully responsive before being released at the capture location. Trout caught in the traps were released approximately 30 m upstream of the dam.

Trout scales were interpreted for age and occurrence of prior spawning events. After the scales were cleaned and mounted on gum cards, impressions were made on plastic sheets using a heat press. The scale impressions were viewed on a microfiche reader. Growth annuli and spawning checks were interpreted independently by two readers, and only samples interpreted consistently were included for further analysis. Spawning events cause significant resorption of scale tissue, which is evident on scales as a broad and irregular mark that often crosses growth rings. We used the scale analysis to estimate the age distribution, spawning age, and frequency of repeat spawning of the mature portion of the population.

Migratory destination and timing

Radio-tagged trout were located using Lotek Wireless SRX 400 receivers, and their positions were recorded with a hand-held GPS unit. Fish tracking was carried out on foot, from a pick-up truck, from the air with a small plane, and with fixed stations. We tracked trout 2–4 times per week during the spring spawning migration (March to June). During summer, fall, and winter, trout were tracked at approximately monthly intervals. Two telemetry fixed stations were installed in the upper Blitzen River (Fig. 1) to ensure migrating trout would be detected if long-distance movements took place between scheduled tracking. Fish location precision ranged from 40 m, when tracking was carried out on foot and triangulation was possible, to 100 m, if carried out from vehicle. Aerial tracking precision was estimated at about 160 m based on similar aquatic aerial telemetry studies (Roberts & Rahel 2005).

Because of high water and high turbidity during the snowmelt period, it was rarely possible to confirm the spawning location of individual trout. Direct spawning observations were made on three occasions. Although spawning location could not often be confirmed, most trout were redetected multiple times near the upstream-most site. In characterising the upstream-most migration sites, we included only trout that migrated more than one km upstream of their tagging location. The time of arrival was the date that a trout was first detected in the vicinity of its upstream-most detection location.

Trout location coordinates from radio telemetry and PIT tag antenna detections were imported into ArcGIS (Esri, Redlands, CA, USA). Detection locations were related to a 1:24 000 scale BLM stream layer rectified to aerial photographs. The coordinates of each of the trout positions were located along the stream route to determine the distance from the river mouth in river kilometres (rkm). Detection locations and tagging records were combined in a database to analyse migrations. Individual migration histories were constructed by plotting the detection locations against the date and time (Anderson 2009). Trout were assigned to the lower river or middle river group based on their capture location.

Migration rates

Migration rate was estimated for trout that were PIT tagged at Sodhouse (rkm 6), Busse (rkm 35), or Grain Camp (rkm 48) dams and subsequently detected at an upstream, open-channel PIT tag reader. The migration rate was calculated by dividing the distance travelled to the PIT tag reader by the time in transit (km per day). Only the initial migration of each fish was considered to prevent problems with repeated measurements on individuals.

Seasonal migrations

We evaluated the migrations of PIT-tagged fish with stationary, swim-through antennas and by scanning recaptured fish with hand-held tag detectors. PIT tag antenna arrays were installed in April 2007 at Page Dam (rkm 67) and in June 2007 at Busse Dam (rkm 35), Grain Camp Dam (rkm 48), and Cato Bridge (rkm 0, Fig. 1). At each of the three dams, one antenna was located 30–50 m downstream of the dam, a second antenna was set in the downstream entrance of the fish ladder, and a third antenna was placed near the upstream exit of the ladder. The antennas below the dams spanned the entire river channel (10–15 m wide), with the bottom of each antenna following the contours of the channel bed and the top a maximum of 0.7 m above it. During most flows, the detection field filled the entire wetted channel, and at high flows, only the upper portion of the water column was outside the detection field. Antennas in the fish ladders matched the dimensions of the ladder. Cato Bridge had two 0.7 by 7-m semi-rigid rectangular antennas with detection fields that filled most of the channel except the area near each bank. The antenna read ranges were checked weekly during the high-flow spring season and monthly the rest of the year. The Busse antenna had periodic power failures in the summer of 2007, and the Grain Camp antenna was damaged from ice formation and was not functioning from November 2007 through February 2008.

Migratory patterns were summarised for trout PIT tagged in the first year of the study and redetected in subsequent years of the study. Individual migration histories were recreated based on the sequence of detections by the PIT antennas. Time, location, and direction of movements were summarised by month and compared with temperature and discharge conditions.

Statistical analyses

A mixed linear model (Proc Mixed; SAS Institute Inc., Cary, NC, USA) was used to evaluate the influence of fork length, temperature, discharge, the number of dams passed (dams), the tagging method (tag), and random effects on migration rate. Mean temperature for each trout's migration was calculated from the temperature logger at Page Dam (rkm 67), and mean discharge was calculated from Page Springs Weir gauging station data. The number of dams passed was included to evaluate the cumulative effect of these structures on trout migration rate. To evaluate the effect of radio tagging, migration rates of trout tagged with both radio tags and PIT tags were compared to those with PIT tags only by including an indicator variable in the regression. Although migration rates were calculated for trout moving through different parts of the river, we considered that they were comparable given a relative uniformity of river gradient and flow velocities.

Preliminary diagnostic scatter plots indicated the need to $\log_e$ transform the response variable, migration rate (Ramsey & Schafer 1997). Following transformation, the model appeared to meet the model assumptions of normality and equal variance based on a normal QQ-plot and a residual versus fit plot. A correlation matrix of the covariate parameters was examined for potential multicollinearity. To select the best model given the limited sample size, all combinations of models with three parameters or less, including a null model, were evaluated using Bayesian information criterion (BIC) selection process. We used BIC model selection over a step-wise selection approach because the former method is able to identify numerous potentially adequate models, whereas the latter only selects a single model. BIC was used in favour of Akaike's Information Criterion because the BIC has a larger penalty for inclusion of insignificant coefficients (Ramsey & Schafer 1997). For the top model, the parameters were tested for interactions. All interaction terms were removed because none had *P*-value of 0.05 or less. Cook's distance was calculated to determine if there were outliers that influenced the results. We selected Cook's distance over other statistics because it detects observations that have either large studentized residual, high leverage, or both (Ramsey & Schafer 1997). Based on the low Cook's distance values, no outliers were considered to be influential on the final model. Although not part of our original question, we were concerned about the possible bias of migration distance and year effects on the test. We added a term for year and a term for migration distance to the final model to determine if it changed the results or if either of these terms was significant.

To determine if trout that were caught and radio tagged in either the lower or middle river migrated to the same upstream reaches (presumably to spawn) and arrived simultaneously, two-sample *t*-tests were used to compare both the location of the upstream-most sites (in rkm) at which radio-tagged trout were detected and the dates that they were first detected in that vicinity. Trout that did not migrate at least one km and lower river trout that did not move past rkm 67,

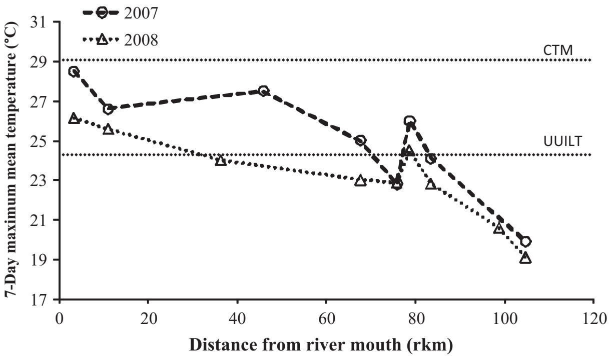

Fig. 2. Seven-day max. mean temperatures for the 2007 and 2008 at ten locations in the Blitzen River. The ultimate upper incipient lethal temperature and critical thermal maximum temperature for redband trout are shown for context. Temperatures warm in the upper river (headwaters to rkm 79), cool moderately in the middle river (rkm 79–67), and warm considerably in the lower river (rkm 67 to river mouth).

below which there is little potential spawning habitat, were excluded.

Results

Environmental conditions

Summer 7-day max. mean temperatures in the lower river exceeded 28 °C in 2007 and 26 °C in 2008 but were much cooler in the upper river (Fig. 2). Summer water temperatures in the Blitzen River generally showed a longitudinal warming pattern from upstream to downstream. The upper river (rkm 79–105) had 7-day max. mean temperatures from 20 to 26 °C in 2007 and 19 to 25 °C in 2008. The river cooled notably at Page Springs (rkm 77) to a 7-day max. mean of 23 °C during both summers. The lower river (rkm 1–67) had 7-day max. mean temperatures from 27 to 29 °C in 2007 and 24 to 26 °C in 2008. Mean temperatures ranged from 0 to 3 °C throughout the river during December and January. In winter, the temperature was slightly warmer in the upper river, and Page Springs appeared to have a mild warming influence.

Fish tagging and scale analysis

A total of 476 trout were trapped and an additional 47 were angled in 2007; 60 were caught in the traps and 35 angled in 2008; and 69 caught in traps and 21 angled in 2009 (Table 1). We tagged 96 redband trout from 272 mm to 560 mm in fork length (FL) with radio transmitters and 611 trout over 100 mm in fork length with PIT tags (all but three radio-tagged trout were also PIT tagged). Radio tag weight averaged 1.4% of the body weight of the fish and ranged from 0.5 to 2.5%. Scales were analysed for 257 trout, which was 36% of all trout captured. Scale readers had

Table 1. Number of trout caught at each location in traps and by angling in 2007 and 2008.

	2007		2008		2009	
Capture location	Trap	Angle	Trap	Angle	Trap	Angle
Sodhouse dam	81	2	6	1	15	4
Busse dam	221	12	39	13	19	14
Grain camp dam	10	29	–	2	–	0
Page dam	164	2	15	5	34	1
Upstream of dams	0	2	0	14	0	1
Total	476	47	60	35	69	21

different interpretations of 42 scales, so those were removed from the sample, leaving 215 usable scale samples.

Trout ranging in size from 115 to 560 mm in fork length migrated upstream during the spring seasons of 2007 to 2009 (Fig. 3). Fish size distribution was bimodal, and according to the scale analysis, included smaller age 1–2 trout and larger age 3–5 trout. Scales

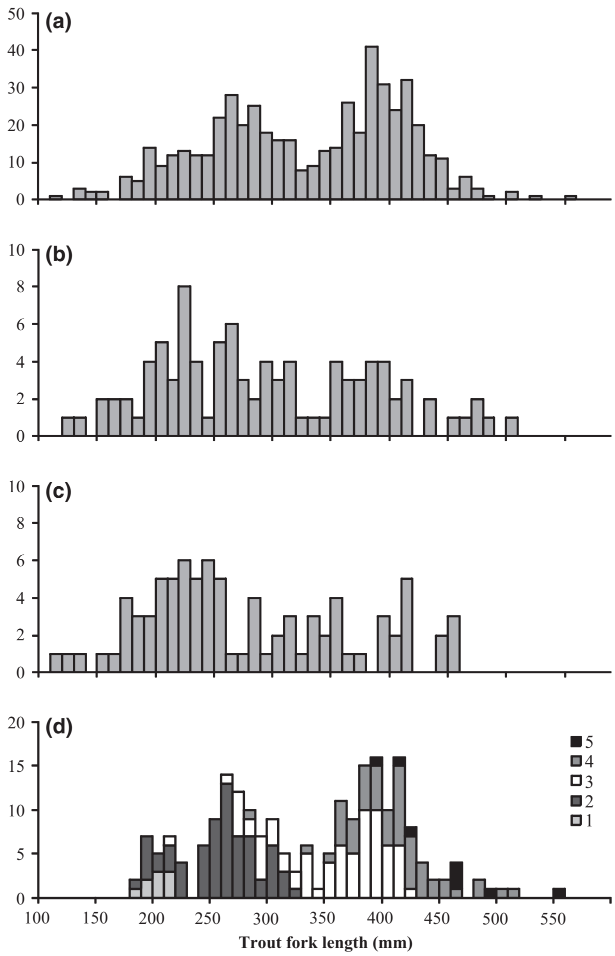

Fig. 3. Histogram of redband trout lengths for (a) all trout captured in 2007, (b) all trout captured in 2008, (c) all trout captured in 2009 and (d) the subset of fish from 2007 and 2008 that had ages interpreted from scale samples.

indicated that none of the trout had spawned prior to age 3. Fifty-two per cent (26 of 50 scales) of age 4+ trout had had spawning checks at age 3. Of six age 5+ trout, three had spawned once before, two had spawned twice before and one had not spawned. The evidence from scale analysis for maturation size was consistent with our observations of gonad development during radio tagging surgery and of spawning coloration. Among 96 radio-tagged trout, 83 (FL 308–560 mm) were spawners, 2 (FL 272–280 mm) were immature, and 11 (FL 272–410 mm) were unknown. On the basis of both scale evidence and field observations, we decided to consider migrating trout under 300 mm in fork length as sub-adults and those over 300 mm as adults. While it is likely that some fish did not conform to this size-at-maturity threshold, it was important to apply a consistent rule to identify immature 'sub-adult' fish.

Migratory destination and timing

Radio-tagged trout were redetected an average of 1.5 times per week in 2007, 1.7 times per week in 2008 and 3.3 times per week in 2009. Of 93 radio-tagged trout, 21 (23%) migrated upstream less than 1 km, 17 (18%) migrated between 1 and 10 km, 16 (17%) migrated between 10 and 25 km, 25 (27%) migrated between 25 and 50 km, and 14 (15%) migrated between 50 and 91 km. Among the trout that migrated upstream over 1 km, 41 were tagged in the lower river and 31 were tagged in the middle river. Sixteen (39%) of the lower river trout were never detected in the middle or upper river and therefore were unlikely to find suitable spawning habitats (Fig. 4). Of those trout that ended their migration in the lower river, nine migrated up to dams that they never passed. Because the fish that did not make it out of the lower river likely did not spawn or spawned in marginal substrates, they were excluded from the test comparing spawning location and timing. The mean upstream-most spawning location (rkm) for lower and middle river trout did not differ ($t = 1.56$; d.f. = 55; $P = 0.13$) (84.4 ± 9.8 rkm for lower river trout; 88.4 ± 9.2 rkm for middle river trout). However, lower river trout arrived at their upstream-most detection site significantly ($t = 2.57$; d.f. = 55; $P < 0.01$) later in the season (May 24th ± 18.3 days) than middle river migrants (May 12th ± 17.2 days). Five trout migrated into the tributary known as the Little Blitzen River and one migrated into Big Indian Creek, while all other trout remained within the Blitzen River mainstem.

Migration rates

Migration rates of 73 PIT-tagged fish ranged from 0.24 to 25.58 km per day and averaged 4.2 km per day. The

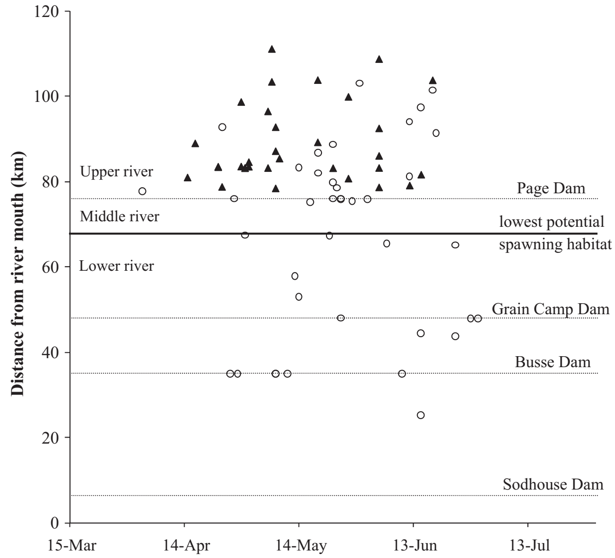

Fig. 4. Location of the upstream-most site and date of arrival for radio-tagged migratory trout from the middle river (▲) and lower river (○). Dotted lines represent diversion dams on the Blitzen River. Solid line represents boundaries between the lower, middle and upper rivers. Little spawning habitat exists in the lower river.

Table 2. Bayesian Information Criteria scores for the top twelve regression models and the null model explaining variation in trout migration rate.

Bayesian information criterion	Independent variables in model
195.0	Fork length discharge
198.0	Fork length discharge tag
199.2	Fork length temperature discharge
199.2	Fork length discharge dams
199.5	Fork length temperature
201.6	Fork length
202.1	Fork length temperature tag
203.4	Fork length temperature dams
205.0	Fork length tag
205.6	Fork length dams
208.9	Fork length dams tag
223.7	Discharge dams
229.5	Null

best explanatory model, based on BIC, included fork length and stream discharge. Table 2 shows the BIC scores for the top 12 models and the null model. The top 11 models all included fork length, and discharge was included in the top four models. Given that fork length and discharge were significant in all models in which they occurred and that the model with only these parameters has a better BIC score than the rest, these two explanatory variables were chosen for the final model. Neither year effects ($P = 0.41$) nor migration distance ($P = 0.63$) were significant when modelled with these variables, and the significance of fork length and discharge was unchanged. The model had an R^2 value of 0.45. In this model, each 1-cm increase in trout fork length was associated with an 8.1% (95% CL from 5.5% to 10.5%) increase in median migration rate, while each 1 $m^3{\cdot}s^{-1}$ increase in mean discharge was associated with a 13.8% (95% CL from 5.3% to 23.3%) increase in median migration rate. However, discharge was negatively correlated with temperature ($r = 0.71$) because high temperatures occurred when discharge was dropping late in the spring.

Seasonal migrations

Migrations observed from PIT tag detections revealed a distinct seasonal pattern. Slightly over half of the trout PIT tagged in the lower river migrated upstream at least 10 km during the spring (51% in 2007 and 60% in 2008). Twenty-four (4%) PIT-tagged trout were detected in subsequent study years, thus providing information about multi-year migrations (Fig. 5). Of those 24 trout, 17 (71%) were small sub-adults when they were first captured. In spring, these 24 trout moved upstream during the high-flow period from March to June. In summer, they remained in the middle or upper river and did not make migratory movements, as indicated by the lack of detections at the PIT tag readers. In fall, as water temperatures cooled, they moved back downstream. A second upstream migration was recorded for 16 of these trout during spring of the second year, and four individuals repeated the upstream migration for a third consecutive spring (Fig. 6). The antenna at rkm 1 only detected three trout (Fig. 5). Detection efficiency for most antennas ranged from 60% to 95%, but the Busse Dam fish ladder antennas had 20–45% efficiency owing to interference from metal in the ladder. The poor performance of the antenna at Busse Dam may have caused us to underestimate the proportion of tagged trout that migrated to this part of the river.

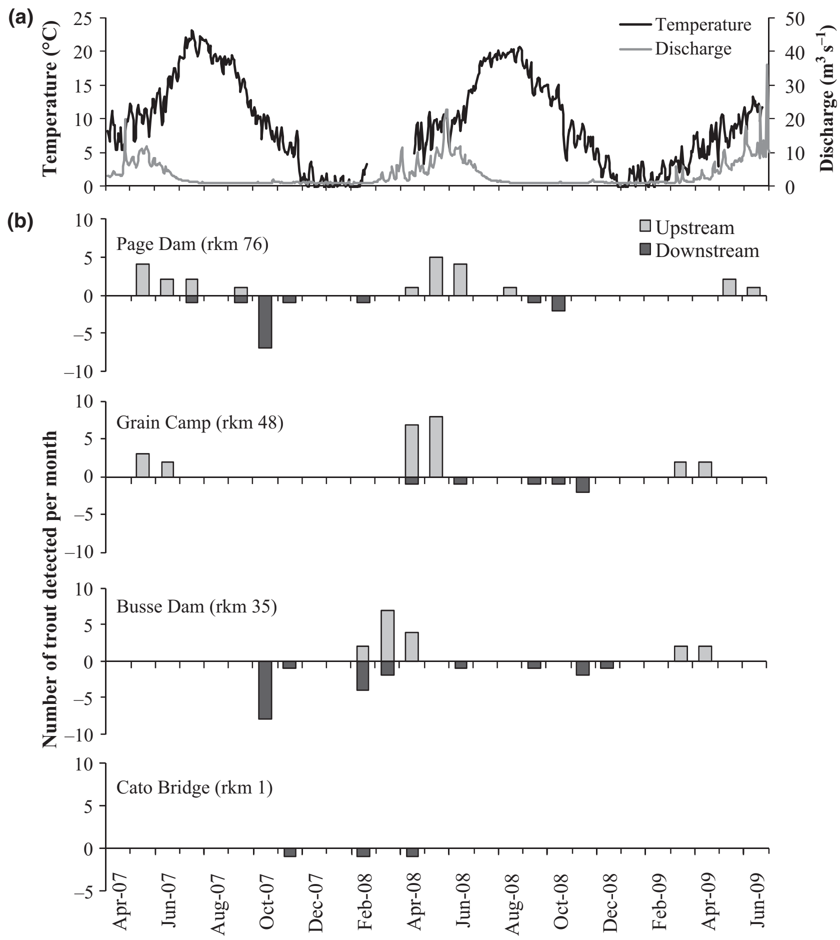

Fig. 5. (a) Mean daily temperature recorded upstream of Bridge Creek and mean daily discharge at the Page Springs Weir compared to (b) directional movements of 24 redband trout passive integrated transponder (PIT) -tagged in 2007 with detections at four different locations in the Blitzen River in subsequent years. The vertical axis depicts the number of fish detected at each PIT antenna location each month, where negative numbers represent downstream moving trout and positive numbers represent upstream moving trout. The horizontal axis shows a common date for both panels.

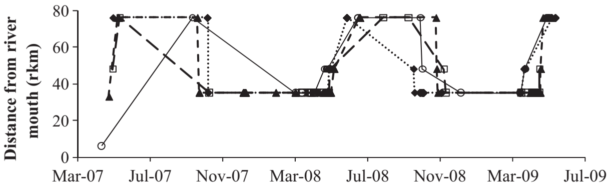

Fig. 6. Migrations of four trout that were tracked from 2007 to 2009. All four were sub-adults at the time of capture. The vertical axis indicates the detection location in rkm distance from the mouth, and the horizontal axis indicates the detection time. Dotted lines connect the nodes for clarity but do not indicate known trout locations between successive detections.

Discussion

Blitzen redband trout made long-distance (1–91 km) upstream migrations in the spring, and some trout made multiple migrations during the course of the study. Adult trout from the lower river and middle river migrated to the same river segments to spawn, but middle river trout tended to arrive at their spawning destinations earlier in the season. The rate of migration was related to fork length, which may be partially attributable to the fact that many of the smaller fish were immature and larger fish were spawners. River discharge, also positively associated with migration rate, may serve as one cue trout used to make their migration. Trout made upstream migrations in the spring, and a fraction made return downstream migrations in the fall. Movement appeared to be fairly restricted during the summer and winter periods.

The migration of adult trout most likely involved the search for suitable spawning substrates, which were rare and, where present, highly embedded with fines in the lower river. Although lower river fish had a much wider total distribution of upstream migration extents, many of these fish, with delayed or failed passage at dams, were likely not successful spawners. Given the limited spatial distribution of spawning substrates in the Blitzen River, it may not be surprising that the radio-tagged adult trout migrated to the same river segments regardless of whether they were in the lower or middle river prior to the spawning migration. Lower river trout, which travelled much farther and encountered numerous diversion dams, arrived at their migratory destinations an average of 12 days later in the season. For salmonids, breeding time is highly heritable, and differences between early and late spawners within a given season can limit gene flow between groups (Hendry & Day 2005).

The relationship between redband trout migration rate and fork length may be partially explained by the fact that both swimming performance (Webb et al. 1984) and energy efficiency (Hinch & Rand 1998) increase with the body length of migrating salmonids. Also, scale analysis indicated that Blitzen redband trout do not reach maturity until age 3+. Because larger trout (FL > 300 mm) were more likely to be sexually mature, stimuli for migration and migratory timing may have been different compared with smaller sub-adult (FL < 300 mm) migrants. Selective pressures, such as mating synchrony, specific seasonal requirements for egg development (de Gaudemar & Beall 1998) and offspring emergence patterns that result in competitive advantages (Einum & Fleming 2000), are likely to influence spawning timing. As a result, spawning fish may reasonably be expected to make more direct movements to reach spawning habitats, while immature fish may be more opportunistic in finding transitional rearing habitats, thus moving more slowly up river.

The positive relationship between river discharge and upstream migration rate suggests, as Trépanier et al. (1996) reported, that elevated discharge may serve as an environmental cue for the spawning migrations of trout. However, because changes in river discharge co-occur with changes in temperature and photoperiod, it is impossible to determine from the results of our study which variable may be the most important cue for trout migration. Independently of the factor or factors that triggered trout migration, most of the large-scale upstream migration we recorded occurred during the spring snow-melt period, and only downstream movements to winter habitat were detected during low-flow conditions. Under high-flow conditions, fish have access to additional spawning habitats in tributaries and gravel bars that are dewatered during lower flow. Although current velocity increases with discharge and can raise the energetic cost of fish migration (Hinch & Rand 1998), deeper water and higher turbidity create cover from mammalian and avian predators during migration (Monnot et al. 2008). Furthermore, high discharge may be necessary for fish to negotiate barriers or difficult river reaches (Rand & Hinch 1998).

Tag type, radio transmitter versus PIT, did not affect the migration rate of redband trout in this study. Despite the fact that many studies have determined that radio tags do not affect salmonid migration rates, behaviour or swimming performance (Swanberg & Geist 1997; Jepsen et al. 2003; Matter & Sandford 2003), we considered it was important to evaluate the tagging methods used in our study. Although it was not possible to compare the performance of radio-tagged trout to true control fish with no tag, PIT tags were chosen as the control because they are much smaller, lighter, and have no external antenna. PIT tags have also been demonstrated to have limited effects on growth, survival or behaviour of juvenile salmonids (Brannas et al. 1994). On the basis of this evidence, we conclude that the tags we used did not have a significant effect on the migratory patterns and rates observed.

The number of dams that trout passed during migration was not a significant factor in determining the rate of migration. This was a surprising result given that long median delays were observed for PIT-tagged trout at Busse and Grain Camp dams, and differences in upstream migration rate through open-water segments versus dammed segments was apparent for many of the radio-tagged trout (see Anderson 2009). On the basis of this evidence, we cannot conclude that the dams do not affect trout migration. Instead, the particular type of dam may have been more influential to the migration rate than the total number of dams because the passage delays among the dams were significantly different (Anderson 2009).

We were not surprised that large redband trout migrated upstream in the spring to find suitable spawning habitats, but the sub-adult migration was unexpected. Field data and scale analysis indicated that trout over 300 mm were likely sexually mature in the spring, but those smaller than 300 mm were predominantly immature. Adult and sub-adult fish migrated upstream at the same time of year but for different purposes. Whereas the migration of adult trout was likely to be primarily for spawning purposes, sub-adults likely migrated in search of suitable summer habitats. The adults may have had the secondary benefit of being in favourable habitat for postspawning recovery. Sub-adult trout with subsequent years of PIT tag detections revealed a common pattern of upstream migration in the spring and downstream migration in the fall, and some made multiple migrations. This migration pattern is exemplified by the individual detection histories of four trout (Fig. 6).

Salmonids that make seasonal migrations typically move to habitats that optimise foraging and growth conditions during warm seasons and move to habitats with cover, deep pools, and low energetic demands during cold seasons (Bjornn 1971; Schlosser 1995). The lower river (and possibly Malheur Lake when full) likely offers good foraging opportunities for piscivorous fish like trout, as prey fish such as cyprinids (Bisson & Bond 1971) are confined to the lower river and Malheur Lake. The ability to utilise this food source during the fall and spring may help explain both the exceptional size-at-age of trout in this study and the purpose of the migration to the lower river. Redband trout have been reported to over-winter in the same segments as their summer habitat, even in cold climates (Muhlfeld et al. 2001). In the Blitzen River, where low temperatures and surface ice was found through much of the river, some redband trout remained in the middle or upper river during winter while others migrated to the deep pools and slow water in the lower river.

The upstream spring migration of sub-adult trout is one indication that the middle and upper rivers offer more suitable conditions to trout during the summer than the lower river. The migration is likely to improve trout fitness by giving them access to good foraging opportunities and favourable thermal conditions. During both summers of the study, temperature in the lower river exceeded redband trout's ultimate upper incipient lethal temperature of 24.3 °C, determined by Bear et al. (2007), and approached the critical thermal maxima reported by Rodnick et al. (2004). Although rainbow trout in arid streams have been observed to use micro-habitat thermal refugia in warm stream reaches, such warm reaches are often associated with low trout densities (Li et al. 1994; Ebersole et al. 2001). We did not evaluate the food base during this study, but warm stream reaches with poor riparian conditions tend to have macro-invertebrate communities with low forage quality (Tait et al. 1994). The metabolic rates of redband trout are also strongly temperature dependent, with optimal growth occurring in the range of 12–16 °C (Bear et al. 2007). Although the 7-day max. mean temperatures in the middle and upper rivers exceeded the optimal growth conditions, temperatures were more frequently in the optimal growth range than in the lower river. The movement patterns we recorded are consistent with the hypothesis that sub-adult redband trout underwent migrations for refugia from stressful temperatures or to take advantage of areas with temperatures that maximised growing conditions. Extensive seasonal migrations have also been described for bull trout (*Salvelinus confluentus*) that emigrated from stream segments with high temperatures (Swanberg 1997; Baxter 2002; Starcivich et al. in press).

Movement tracking studies of redband trout in other Great Basin streams have documented spawning migrations (Kunkel 1976; Tinniswood 2007), but sub-adult migrations, such as those observed in the Blitzen River population, have not been reported. Northcote (1997) describes this as a three-stage migration cycle in which salmonids move between feeding habitats and survival habitats numerous times before making a spawning migration. River systems connected to habitats with both appropriate thermal conditions and foraging opportunities year-round, such as lakes, may support a migratory life history that only involves large-scale movements between rearing and spawning habitats (see Meka et al. 2003). The cycle of repeated sub-adult migrations between summer feeding and winter survival habitats before first spawning, as we observed, may occur where there are consistent and extreme seasonal shifts in temperature and spatially separated habitat patches. Our findings underscore the importance of local conditions and of spatial and temporal heterogeneity of habitat patch distribution in the expression of migratory life histories.

The migratory population of Blitzen River redband trout represents an important life history, which was likely more prevalent in Great Basin populations in the past (Bowers et al. 1999). The results of this study suggest that trout migration patterns are related to the life stage, seasonally fluctuating physical stream conditions, and spatially segregated habitats. Anthropogenic factors, particularly instream water withdrawal, have reduced suitable habitats and their connectivity to the detriment of migratory life histories. Salmonid populations with multiple life history strategies are likely to be more resilient to changing environmental conditions (Rieman & Dunham 2000), and the conservation and restoration of conditions that support migratory behaviour in trout should be a high priority.

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