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Adfluvial and fluvial life history variations and migratory patterns of a relict charr, *Salvelinus confluentus*, stock in west-central Idaho, USA

Watry CB, Scarnecchia DL. Adfluvial and fluvial life history variations and migratory patterns of a relict charr, *Salvelinus confluentus*, stock in west-central Idaho, USA.
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Abstract – Life history strategies and migratory patterns of 71 adult radio-tagged bull trout, *Salvelinus confluentus*, were studied in the Secesh River watershed within the South Fork Salmon River (SFSR) sub-basin in west-central Idaho, USA during 2003 and 2004. In both years, upstream migrations occurred during late June and early July, migrations into two spawning tributaries during late July and early August, spawning from mid-August through mid-September, and rapid downstream (postspawning) migrations from late August to mid-September. Primary over-wintering areas were Loon Lake, the lower Secesh River (downstream of Loon Creek), and the lower SFSR (downstream of the confluence with the Secesh River). Loon Lake evidently provides sufficient production to allow the adfluvial life history strategy to persist and predominate in the Secesh River, while the fluvial life history strategy was previously found to predominate in the nearby East Fork SFSR. Adfluvial, nonconsecutive-year migrations were the predominant life history strategy. Only seven fish made consecutive-year migrations to Lake Creek; however, only one of these fish, a female, utilised a spawning tributary in both years and showed spawning tributary fidelity. Three consecutive-year migrants and three in-season migrants showed over-wintering site fidelity by returning to Loon Lake in September, 2004. The life history variations observed for bull trout in the Secesh River watershed are similar to those observed for bull trout throughout their range and to those of other charr species worldwide, yet the development of distinct migration patterns demonstrate the adaptability of the species to a range of available habitats.

Key words: charr; migration; bull trout; *Salvelinus*; *Salmonidae*

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Introduction

Fish stocks of the genus *Salvelinus* (Family: Salmonidae) in the Arctic charr, *Salvelinus alpinus*, and Dolly Varden, *Salvelinus malma*, complexes exhibit great genotypic, phenotypic and life history variation across their ranges (Behnke 1984; Taylor et al. 1999). Phylogenetic divergence has occurred extensively in these species complexes since the early-Pleistocene and has been associated with the episodic advances and retreat of glaciers (Behnke 1980; Magnan et al. 2002; Power 2002). Changing environmental conditions and habitat characteristics over geologic time, and more recently, have favoured the development of diverse life history strategies, resulting in stock-specific adaptations as well as morphological and ecological plasticity within and among stocks (McCart 1980; Näslund 1992; Hindar & Jonsson 1993).

The bull trout, *Salvelinus confluentus*, a piscivorous charr of the Dolly Varden complex native to much of the Pacific north-west region of North America (Cavender 1978; Haas & McPhail 1991), exhibits a

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variety of life history strategies typical of charrs, including adfluvial potamodromy (migrations between lake or reservoir systems and rivers; Fraley & Shepard 1989; Olmstead et al. 2001), fluvial potamodromy (migrations between rivers; Hogen & Scarnecchia 2006), residency (Chandler et al. 2001; Nelson et al. 2002), and in a few instances, anadromy (Baker et al. 2003). Considerable research has been conducted on life history strategies and habitat use of numerous stocks during the past 15–20 years (e.g. Mackay et al. 1997; Brewin et al. 2001). However, in many localities, little is known about stock-specific life history strategies, migration patterns and habitat use.

The evolution of different migratory forms has enabled bull trout to occupy spatially diverse habitats and optimise reproductive potential by maximising growth, fecundity and survival in variable environments (Northcote 1978). Diverse life history strategies may therefore be critically important to the long-term stability and persistence of the species (Rieman & McIntyre 1993; Stowell et al. 1996; Rieman & Allendorf 2001). Continued habitat degradation, the expansion of nonnative species, and prolonged habitat fragmentation has reduced the distribution and abundance of bull trout in many localities (Rieman et al. 1997).

In the north-western United States and Canada, the range of bull trout has continued to contract and become fragmented over the last century, particularly in the more temperate southern portions (Nelson et al. 2002). Specific factors contributing to this range contraction and fragmentation include loss or alterations of critical spawning and rearing habitat (Rieman & McIntyre 1993, 1995; Rieman et al. 1997), competition with introduced nonnative species, and hybridisation and introgression with nonnative brook trout (*Salvelinus fontinalis*).

The South Fork Salmon River (SFSR) sub-basin in central Idaho, USA, is considered a stronghold for the species in the interior northwest (U.S. Fish and Wildlife Service 1998). Hogen & Scarnecchia (2006) described a primarily fluvial life history strategy for bull trout in the East Fork South Fork Salmon River (EFSFSR), with a minor adfluvial component associated with a 60-year old, 2 ha flooded mining pit. However, in the neighbouring Secesh River, little is known about any aspects of bull trout life history and ecology, including the location of spawning and over-wintering areas, migration patterns and run timing, as well as environmental factors that affect spawning and migration timing. By extending the type of investigation conducted by Hogen & Scarnecchia (2006) to a second nearby watershed with different habitat characteristics within the SFSR sub-basin, we sought to gain additional insight regarding stock discreteness and factors influencing life history variations in bull trout and charrs in general.

Our objectives were to: (i) identify and characterise life history strategies (adfluvial or fluvial), including the classification of migration patterns and delineation migratory corridors and (ii) assess spatial and temporal distributions of bull trout relative to life history strategies in the Secesh River and its tributaries. The results are discussed in relation to variations in life history strategies observed for migratory bull trout and other migratory charrs worldwide.

Study area

The study occurred within the Secesh River which drains one of four major watersheds in the SFSR sub-basin in west-central Idaho, USA (Fig. 1). The three other watersheds include the lower SFSR, the EFSFSR and the upper SFSR above the confluence with the EFSFSR. The Secesh River watershed encompasses approximately 63,940 ha, or slightly <20% of the SFSR sub-basin (area: 339,940 ha).

The Secesh River is located in the north-western portion of the SFSR sub-basin in an area of primarily granitic geology (Idaho Batholith). Soils are generally sandy and poorly developed with low water-holding capacity and low natural fertility, contributing to low stream productivity (Klamt 1976). The Secesh River flows in a general south-southeast direction from its origin at the confluence of Lake Creek and Summit Creek (two major tributaries) to its confluence with the mainstem SFSR located 1.6 km below the confluence of the EFSFSR and SFSR (Fig. 1). Channel gradients range from <1% along tributaries in the upper Secesh watershed to more than 10% in canyon sections of the main Secesh River. Peak discharge in the Secesh River results from snowmelt runoff during late May and June, and base flows occur from November through March. In Lake Creek, peak recorded discharge was approximately 62.5 and 11.0 $m^3{\cdot}s^{-1}$ on 28 May, 2003 and 2004 respectively. The Secesh River watershed also contains a 60-ha mountain lake (Loon Lake) approximately 3.0 km upstream of the confluence of Loon Creek with the Secesh River (Fig. 1).

Native fish assemblages in the SFSR sub-basin include both resident and anadromous salmonids. Native resident species include bull trout, redband trout (*Oncorhynchus mykiss*), westslope cutthroat trout (*O. clarki lewisi*) and mountain whitefish (*Prosopium williamsoni*). Native anadromous species include endangered Chinook salmon (*O. tshawytscha*) and steelhead trout (*O. mykiss*). Runs of sockeye salmon (*O. nerka*) were historically present into Loon Lake and Warm Lake in the upper Secesh River and SFSR watersheds, respectively, and are now thought to be

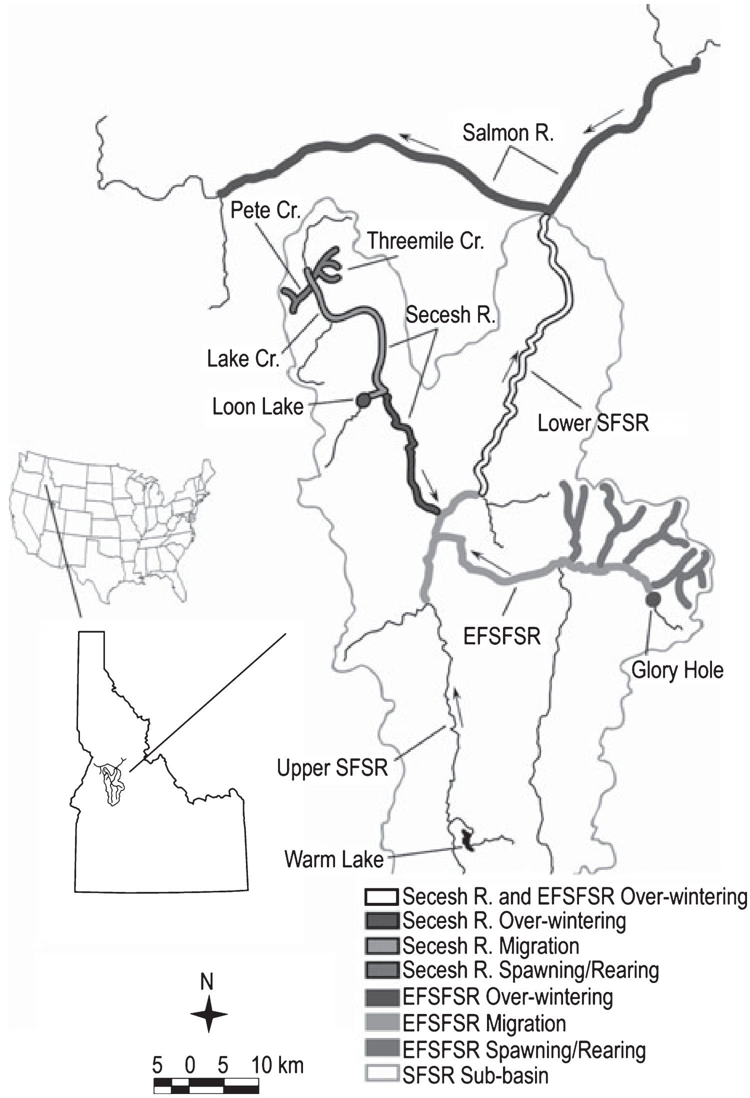

Fig. 1. Secesh River and East Fork South Fork Salmon River (EFSFSR) bull trout over-wintering locations, migration corridors and spawning/rearing areas in the South Fork Salmon River (SFSR) and Salmon River drainages; determined by radio telemetry, 2003–2004 and 1999–2000 developed from Hogen & Scarnecchia (2006).

extirpated; however, relict kokanee (*O. nerka*) populations are still present in these lakes. Introduced, nonnative species include brook trout, mixed cutthroat trout stocks (*O. clarki* spp.), Kamloops rainbow trout, golden trout (*Salmo aquabonita*), lake trout (*Salvelinus naymaycush*) and arctic grayling (*Thymallus arcticus*). Naturally occurring hybridised species include bull trout × brook trout hybrids (hybrids) and cutthroat × rainbow trout hybrids.

Methods

Fish capture

Adult bull trout were captured in the Secesh River watershed mainly by hook and line using a combination of artificial lures, bait with circle hooks and artificial flies. This sampling method previously proved effective, with minimal harm to the fish, when collecting bull trout in the EFSFSR (Hogen & Scarnecchia 2006).

In 2003, fishing occurred almost daily between 19 June and 15 August either in the Secesh River or Lake Creek. Sampling at these particular locations and times was intended to target fish during their upstream prespawning migrations. From past observations, spawning was thought to occur after 15 August. From this sampling, 24 prespawn bull trout and one putative hybrid were selected to be radio-tagged. Putative hybrids were distinguished from bull trout and brook trout by using multiple external phenotypic traits as described in Markle (1992) and Watry (2005). In addition to these fish, 20 postspawn bull trout captured at the Nez Perce Tribe's rotary screw smolt trap on Lake Creek between 23 August and 7 September were selected for radio-tagging, for a total of 45 fish. Postspawn fish were identified by gently stripping the fish for gametes to verify gender and reproductive condition, although gender was not verified for all fish. Other indicators identifying postspawn fish included their emaciated appearance, enervated condition and late date of capture (late August to early September).

In 2004, fishing effort was focused in three locations: Loon Lake, the Secesh River and Lake Creek during the period 12 June to 22 July. From this sampling, 26 prespawn fish, including 16 bull trout, two brook trout, and four putative hybrids in Loon Lake and four bull trout in Lake Creek were selected to be radio-tagged. No postspawn fish were selected for tagging in 2004 because of high mortality rates of this group of radio-tagged fish in 2003.

Following capture, fish selected for tagging were immediately transferred to perforated stream tubes (90 cm × 10 cm or 90 cm × 15 cm polyvinyl chloride pipe with sliding door on one end) and submerged in the stream for at least 15 min prior to additional handling. Sampling and surgical procedures typically followed immediately thereafter. However, for fish caught during mid-day heat, surgeries were postponed until early evening when cooler air temperatures prevailed. For fish caught late in the evening, surgeries were postponed until the next morning.

Radio-tag specifications

Transmitters with specific radio frequencies allowed identification of individual fish. In 2003, 45 fish were implanted with Advanced Telemetry Systems (ATS) F1825 and F1835 radio transmitters (Table 1). In 2004, 26 fish received ATS F1815 radio-telemetry transmitters (Table 1). As a rule, the weight of the transmitter did not exceed 2% of the total body weight of the fish to be tagged (Winter 1996). In 2003, both types of tags had duty cycles that transmitted signals for 6 h per day for four consecutive days, and did not transmit for three consecutive days per week. The short battery life of 200 days for the F1825 transmitters used in 2003 only allowed for a single spawning and over-wintering season to be monitored. In 2004, the F1815 radio-tags had a duty cycle that transmitted signals for 6 h per day, 7 days per week. The limited duty cycle of all tags made it impractical to utilise a fixed receiving station.

All tags were outfitted with mortality sensors that activated a specific signal equal to twice the normal pulse rate indicating that a fish or transmitter remained motionless for a period of 12 consecutive hours. Mortality signals used twice the battery power, which decreased the effective battery life. The reliability of mortality sensors was uncertain, particularly during winter, because of the natural sedentary behaviour of bull trout at that time of year. Johnson (1980) described observations of Arctic charr behaviour during winter by diving under ice and noted that fish remained relatively motionless by resting on their fins. In such a case, individual fish could intermittently transmit a mortality signal, reducing battery life. Therefore, mortality signals were not considered a positive indication of fish mortality. Multiple sequential contacts of mortality signals were required before inferences regarding potential fish mortality or tag loss were made for individual fish.

Radio-tag implantation

Fish to be tagged were moved from the stream tube and placed into 20 l water containing a solution of 60–80 mg·l^{-1} tricaine methanesulfonate (MS-222). Fish were completely anaesthetised after 2–3 min. Fish were then transferred to a padded, v-shaped cradle and positioned on their dorsum for surgical tag implantation. To ensure complete anaesthetisation throughout the surgical procedure the gills and head were continuously irrigated with MS-222 solution.

The procedure used to implant radio-tags was similar to the shielded-needle technique described by Ross & Kleiner (1982) as modified by Hogen & Scarnecchia (2006). The initial 4 cm incision was made 1 cm from the mid-ventral line, anterior to the pelvic fins. A small separate opening was made for extrusion of the tag antenna. Three surgeon's knots, spaced 1 cm, apart served to suture the incision closed. After the first suture was completed, irrigation of fresh water over the gills was begun to prevent an anaesthetic overdose. A fourth suture at the antenna exit orifice helped prevent irritation from excessive movement of the exterior antenna.

Mobile tracking

Radio signals from tagged fish were received using a directional, three-element Yagi antenna and either an

Table 1. Specifications of radio-tags used in 2003 and 2004.

Model no.	Year	No. of fish tagged	Effective battery life (days)	Tag weight (g)	Minimum body weight (g)	Frequency range (kHz)	Dimensions (mm diameter × mm length)
F1815	2004	26	200	7.5	375	150	12 × 36
F1825	2003	30	304	8.0	400	150	12 × 43
F1835	2003	15	957	13.6	680	151	17 × 42

ATS R4000 receiver or a Lotek SRX400 receiver. Radio-tagged fish were tracked between July 2003 and October 2004 during periods of predetermined tag transmission. Weekly tracking was conducted from a vehicle or by foot from July through September 2003 and from June through October 2004. Aerial surveys with fixed wing aircraft were conducted on 20 September and 24 October, 2003; and on 13 June, 8 September and 1 October, 2004.

Fish locations were recorded using a Global Positioning System in the UTM NAD27CONUS coordinate system. Calculated map distances were measured from the mouth of the Secesh River beginning at river km (Rkm) 1098.6. Locations referenced as Rkm were recorded for each captured fish, and capture locations were considered the initial point of contact for each fish. Subsequent contacts were calculated as distances travelled from the initial point of contact.

When not in spawning tributaries, fish locations accurate to within approximately 50 m were deemed adequate to meet study objectives. When in spawning tributaries, triangulation helped determine precise locations to help make general observations of radio-tagged fish, particularly during the known spawning season beginning in mid-August, as identified from other studies (Shepard et al. 1984; Schill et al. 1994; Swanberg 1997; Hogen & Scarnecchia 2006). Spawning for this study was defined as any activity that demonstrated fish were participating in the spawning process, including the construction of redds, the presence of redds with fish present, the pairing of fish in small headwater tributaries during the fall spawning season, and aggressive behaviour of fish while guarding a redd. We attempted only to identify spawning areas, not to quantify spawning habitat or to detect population trends.

No surveys were conducted during winter in 2003 and 2004 because of access problems and the inability to detect transmitter signals from the air through ice and snow. Johnson (1980) suggested the winter activity of arctic charr was negligible, and there is supporting evidence that bull trout display similar behaviour. Hogen & Scarnecchia (2006) observed that fluvial bull trout in the mainstem Salmon River and lower SFSR moved <1 km during winter. Elle et al. (1994) and Schill et al. (1994) reported negligible movements of 50–100 m within individual habitat units during winter on the mainstem Salmon River for Rapid River bull trout. In 1992, all fish reached their over-wintering destination by early October (Schill et al. 1994). In the Blackfoot River, Montana, fluvial bull trout movements during winter never exceeded 300 m (Swanberg 1997). As a result, winter movements were assumed to be minimal and localised; therefore, fish locations during spring 2004 relative to the last known locations during fall 2003 were used to corroborate over-wintering locations.

Life history strategies and migration patterns

Movements of radio-tagged fish were grouped into life history strategies (adfluvial or fluvial), and within these strategies, migration patterns were identified. Because capture locations differed between 2003 and 2004, migration patterns were identified and evaluated separately for each year. In a few instances, fish mortality or tag loss made it impossible to assign a specific migration pattern to individual fish.

It was hypothesised that the tendency to manifest an adfluvial (as opposed to fluvial) life history strategy would differ between Secesh River and EFSFSR fish, despite their close proximity, because of the presence of a large lake in the Secesh River watershed in contrast to the man-made impoundment in the EFSFSR watershed (Hogen & Scarnecchia 2006). The null hypothesis was that bull trout winter habitat selection and corresponding life history strategy (adfluvial vs. fluvial) was independent of natal watershed (Secesh River vs. EFSFSR). The hypothesis was tested at the 0.05 level of significance using the chi-squared test, $\chi^2 = \Sigma\ (O-E)^2/E$, where O = observed results and E = expected results (Zar 1999).

Results

Life history strategies and migration patterns

Sixty-four of 71 radio-tagged fish were classified into one of four migration patterns. Based mainly on tagging location and duration of tracking, the four migration patterns identified were: migratory adfluvial, stationary adfluvial (used to describe fish in Loon Lake that did not migrate during the season but would have had to previously migrate to Loon Lake), fluvial and adfluvial-fluvial. In all, 43 fish displayed one of two strictly adfluvial patterns. Twenty-nine fish displayed the migratory adfluvial migration pattern in 2003 (N = 26; Fig. 2) and 2004 (N = 3; Fig. 3) while the stationary adfluvial pattern was exclusively associated with fish captured in Loon Lake in 2004 (N = 14; Fig. 4). Nineteen other bull trout in 2003 (N = 16) and 2004 (N = 3) displayed fluvial migration patterns (Figs 5 and 6). Two fish captured in Loon Lake during June 2004 displayed an adfluvial–fluvial migration pattern (Fig. 7). Specific migration patterns were not assigned to three confirmed prespawn mortalities in 2003 and four apparent mortalities in 2004.

In the most common migration pattern observed (migratory adfluvial), 14 prespawn bull trout captured during July 2003 entered one of two

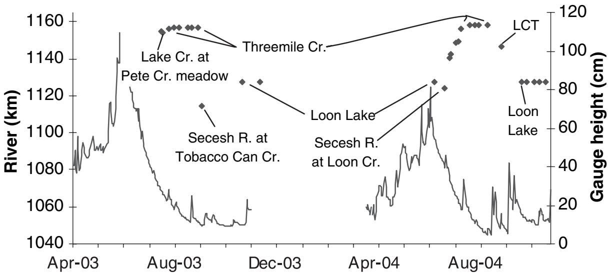

Fig. 2. Representative example of a fish illustrating the adfluvial migratory pattern displayed by 25 bull trout and one hybrid captured during 2003 in Lake Creek ($N = 15$), at the Lake Creek smolt trap ($N = 10$), and in the Secesh River ($N = 1$) in the South Fork Salmon River sub-basin, 2003 and 2004. The 14 bull trout captured in Lake Creek were observed in spawning tributaries while only four of these fish displayed consecutive year migrations, one to a spawning tributary in both years (shown below). Gauge heights were measured on Lake Creek at the Nez Perce Tribes smolt trap (LCT) site (river km 1146.8).

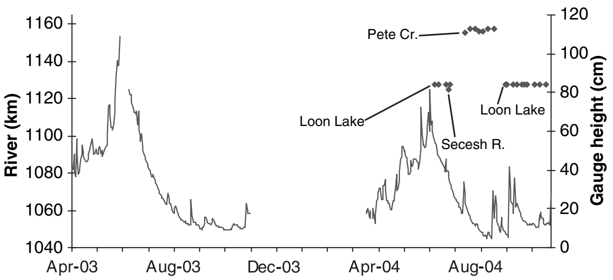

Fig. 3. Representative example of a fish illustrating the adfluvial migratory pattern displayed by three bull trout captured during 2004 in Loon Lake in the South Fork Salmon River sub-basin, 2004. Although only two of these fish were observed in spawning tributaries, all three made successful migrations back to Loon Lake to over-winter. Gauge heights were measured on Lake Creek at the Nez Perce Tribe smolt trap site (Rkm 1146.8).

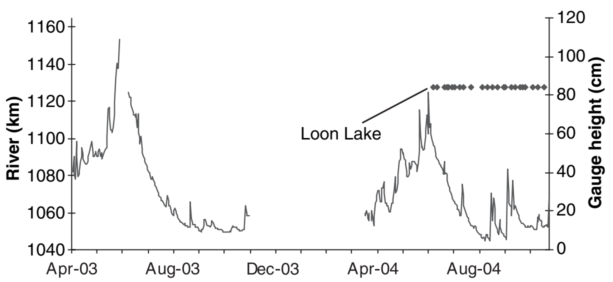

Fig. 4. Representative example of a fish illustrating the stationary adfluvial pattern displayed by 14 fish (eight bull trout, two brook trout and four hybrids) captured during 2004 in Loon Lake in the South Fork Salmon River sub-basin, 2004. Gauge heights were measured on Lake Creek at the Nez Perce Tribe smolt trap site (Rkm 1146.8).

tributaries, remained in the tributary between 5 and 52 days, evidently spawned, exited the tributary, moved downstream, entered Loon Creek and

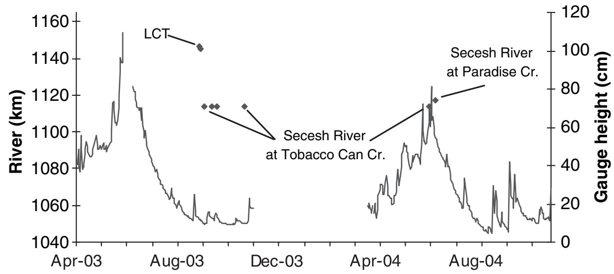

Fig. 5. Representative example of a fish illustrating the fluvial migratory pattern displayed by 10 bull trout captured during 2003 at the Lake Creek smolt trap (LCT) in the South Fork Salmon River sub-basin, 2003–2004. Gauge heights were measured on Lake Creek at the Nez Perce Tribe smolt trap site (Rkm 1146.8).

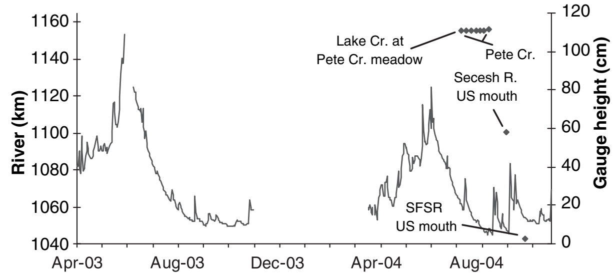

Fig. 6. Representative example of a fish illustrating the fluvial migratory pattern displayed by nine bull trout captured during 2003 ($N = 6$) and 2004 ($N = 3$) in Lake Creek in the South Fork Salmon River sub-basin, 2004. Six of these fish were observed in spawning tributaries in 2003 ($N = 4$) and 2004 ($N = 2$). Gauge heights were measured on Lake Creek at the Nez Perce Tribe smolt trap site (Rkm 1146.8).

migrated upstream to Loon Lake (Fig. 2). One putative hybrid also displayed this general pattern, but was not observed in a tributary and apparently remained in Lake Creek for 47 days before emigrating to Loon Lake. Eleven other bull trout captured and tagged, during August and early September, at either the Lake Creek smolt trap ($N = 10$) or by angling in Lake Creek ($N = 1$) immediately migrated downstream following tagging, entered Loon Creek and migrated upstream to Loon Lake. In all, seven of the 10 fish captured at the Lake Creek smolt trap showed verifiable evidence of gender (three males and four females) and postspawning condition. In 2004, three bull trout captured during June in Loon Lake first moved downstream in Loon Creek from the lake before beginning their upstream migration in the Secesh River to Lake Creek and its tributaries (Fig. 3); one of these fish was not observed in a tributary. In both years, emigration out of tributaries was rapid, and occurred between mid-August and late September. Eleven of 14 bull trout exited small tributaries, evidently after spawning, by 7 September, 2003. Following emigration from the small tributaries, fish were later located during September,

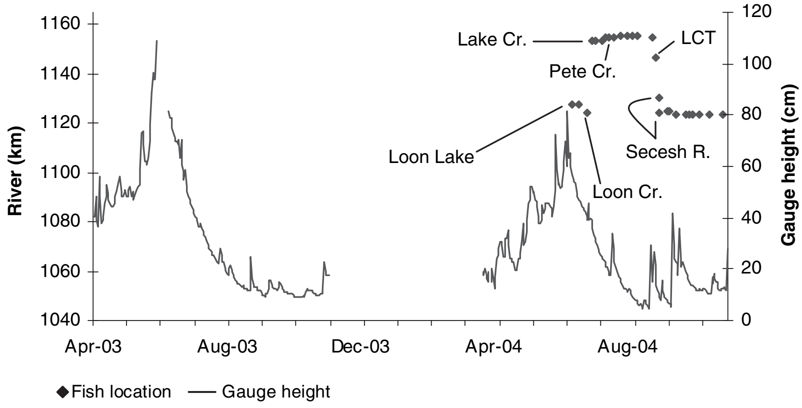

Fig. 7. Representative example of a fish illustrating the adfluvial–fluvial migratory pattern displayed by two bull trout captured during 2004 in Loon Lake in the South Fork Salmon River sub-basin, 2004. Both fish were located in spawning tributaries during the spawning season. Gauge heights were measured on Lake Creek at the Nez Perce Tribe smolt trap (LCT) site (Rkm 1146.8).

October and November in Loon Lake. Mortality rates were 29% for bull trout captured by angling in Lake Creek, with 10 of 14 fish relocated in Loon Lake during June 2004. In contrast, mortality rates were 80% for fish captured at the Lake Creek trap.

In the second most common migration pattern (fluvial) 13 bull trout immediately moved downstream to the lower Secesh River ($N = 11$) or the lower SFSR ($N = 2$) following capture where they remained through November and evidently into winter (Figs 5 and 6). These fish were initially captured and tagged at the Lake Creek smolt trap between 23 August and 7 September, 2003 ($N = 10$), or by angling in Lake Creek during 2003 ($N = 2$) and 2004 ($N = 1$). In all, 80% of the fish initially captured and tagged at the smolt trap showed verifiable evidence of gender (five males and three females) and postspawning condition, whereas the three fish captured in Lake Creek did not show evidence of gender. Ten of the 12 (83%) fish from 2003 were transmitting mortality signals in October and November. One of the two live fish was transmitting mortality signals in June 2004, while the other was not relocated during 2004. Six other bull trout captured by angling in Lake Creek in 2003 and 2004 ($N = 4$ and 2 respectively) entered a tributary, remained in the tributary for up to 46 days, evidently spawned, exited the tributary, and moved downstream to the lower Secesh River in 2003 ($N = 4$) and 2004 ($N = 1$) or the lower SFSR in 2004 ($N = 1$; Fig. 6). Similar to the migratory adfluvial pattern, these fish rapidly emigrated out of tributaries, all fish having exited small tributaries by 7 September. In all, 75% of the fish tagged in 2003 transmitted live signals in November 2003, and two of these fish were relocated in the Secesh River transmitting live signals, evidently without migrating, during 2004.

In the third most common migration pattern (stationary adfluvial) 14 fish captured and tagged in Loon Lake during June 2004 remained there for the duration of the summer (Fig. 4). One (7%) of these fish transmitted a mortality signal within 18 days of being tagged and it could not be determined whether this fish expelled its tag or died. All remaining fish survived in the lake through at least October when tracking was terminated.

In the least common migration pattern observed (adfluvial–fluvial) two bull trout exited Loon Lake in late June and early July in 2004, moved upstream in the Secesh River and Lake Creek, entered a tributary in late July, remained in the tributary between 36 and 39 days, evidently spawned, exited the tributary and moved downstream to the lower Secesh River (Fig. 7). Both fish rapidly emigrated from the tributary during late August and early September, and were later located in the Secesh River during September and October.

The test of over-wintering habitat selection and corresponding life history strategy (adfluvial vs. fluvial) for Secesh River and EFSFSR fish indicated that life history strategy was dependent on natal watershed ($\chi^2 = 34.7$; $P < 0.001$; Table 2). Therefore, a significantly higher percentage of radio-tagged Secesh River fish in the present study were adfluvial than in the radio-tagged fish of the EFSFSR studied by Hogen & Scarnecchia (2006).

Movement to spawning tributaries

Only two small tributaries of Lake Creek in the upper Secesh River drainage were utilised by radio-tagged bull trout in 2003 and 2004. Bull trout were first located on 19 July, 2003 and 21 July, 2004 in

Table 2. Chi-squared contingency table for observed (expected) numbers of fish displaying adfluvial and fluvial migration patterns in the Secesh River (2003 and 2004) and EFSFSR (Hogen & Scarnecchia 2006).

	Adfluvial	Fluvial	Total
Secesh River	48 (33)	19 (34)	67
EFSFSR	5 (20)	36 (21)	41
Total	53	55	108

one of two small tributaries where spawning of nontagged fish was later observed. In each year, one fish was observed to move between spawning tributaries prior to the spawning period. In all, 27 radio-tagged bull trout were observed in spawning tributaries during 2003 ($N = 18$) and 2004 ($N = 9$). Only one of these fish, a female, displayed consecutive-year migrations, and utilised the same spawning tributary in each year.

Prespawn mortalities and tag recovery

Prespawn mortalities and tag recoveries were those confirmed or observed prior to 15 August in each year. In 2003, confirmed prespawn mortalities ($N = 2$) and tag recoveries ($N = 1$) accounted for 12% of all prespawn radio-tagged fish ($N = 25$). During 2004, mortality signals were received from 11.5% ($N = 3$) of all prespawn radio-tagged fish ($N = 26$) although mortalities could not be confirmed. One other radio-tag was recovered on 18 August, 2004 in a small tributary, but the fate this fish could not be determined prior to the spawning season. The carcass and radio-tag of one consecutive-year migrant that over-wintered in Loon Lake was recovered on the Secesh River on 2 August, 2004.

Emigration from Loon Lake

Twelve radio-tagged bull trout emigrated out of Loon Lake during late June and early July 2004. Contacts with fish in Loon Creek occurred within what was assumed to be a short time after emigration from Loon Lake. As such, three fish were located either in Loon Creek or in the Secesh River at the mouth of Loon Creek on 25 June, representing the earliest observed date of emigration. These three fish were consecutive year migrants, one of which was tagged in 2004. Nine of the 12 migrants emigrated from Loon Lake by 2 July, with the latest dates of emigration occurring between 2 and 9 July. Sample sizes were too small to determine precise dates of emigration or migration rates.

Migration periodicity

Sixteen fish tagged in 2003 were relocated in 2004, yet only six of these fish (five bull trout and one hybrid) migrated in 2004. Another bull trout that was PIT tagged and identified as a female in 2003 was recaptured and radio-tagged in Loon Lake in June 2004. Six of these seven consecutive-year migrants over-wintered in Loon Lake whereas the other fish was located in the Secesh River prior to winter in November 2004. Of the seven consecutive-year migrants in 2004, two females utilised spawning tributaries, another fish was repeatedly located in Lake Creek, but was not observed in a spawning tributary, and one fish was a prespawn mortality. Incomplete data for three other fish made it impossible to assess their true migratory periodicity.

Spawning activity

No radio-tagged fish were observed spawning in either tributary (i.e. Pete Creek or Threemile Creek) located in the upper Secesh River watershed, although a few did display spawning behaviours such as pairing and chasing. Spawning locations and period were conditional upon locations of radio-tagged fish relative to observations of nontagged fish. Redds were observed independent of radio-tagged fish locations in both years.

The first paired fish were observed on 18 August, 2003 and 27 July, 2004. In all, 11 redds were positively identified between 24 August and 21 September, 2003 and three redds were positively identified between 17 August and 1 September, 2004. Radio-tagged fish remained in spawning tributaries until at least 23 and 26 August, 2003 and 2004 respectively. In 2003, one radio-tagged fish remained in a spawning tributary until at least 21 September, the latest such observation in both years.

Postspawning movements and mortalities

In 2003, 37 of 39 fish were contacted in Loon Lake ($N = 20$), the Secesh River ($N = 11$), Loon Creek ($N = 3$) and the SFSR ($N = 3$). In all, 24 (57%) postspawning migrants were transmitting mortality signals in November 2003. In 2004, six of 12 migrant fish survived postspawning migrations. Four of these six surviving fish were captured and tagged in Loon Lake, two of which returned to Loon Lake by 8 September displaying over-wintering site fidelity. The other two of these four fish were located in the Secesh River by 15 September. Two other migratory fish that were initially captured in Lake Creek were located in the Secesh River on 8 September. One of these two fish made the single longest individual migration of any radio-tagged fish, travelling a total distance of 113.3 km and was last located near the mouth of the SFSR (Fig. 6). Two consecutive-year migrants which over-wintered in Loon Lake were relocated in Loon Lake during September; both transmitted mortality signals in October 2004.

Over-wintering

Radio-tagged bull trout over-wintered in Loon Lake, the lower Secesh River (below Loon Creek), and the lower SFSR (below the mouth of the Secesh River). In all, 22 of 41 fish (54%) were either last located in Loon Lake in November 2003, or were relocated in

Loon Lake in June 2004; the one radio-tagged hybrid also evidently over-wintered in Loon Lake. Fourteen of these fish survived in Loon Lake until at least June 2004. Two consecutive-year migrants demonstrated over-wintering site fidelity by returning to Loon Lake in September 2004. In 2004, 17 of 22 (77%) fish captured and tagged in Loon Lake during June were relocated in Loon Lake during October. Three of these 17 were migratory bull trout that survived the spawning season and demonstrated over-wintering site fidelity by returning to Loon Lake. Postspawning mortalities of fish in the Secesh River made it difficult to assess actual over-wintering locations for these fish, which were identified as fluvial migrants.

Stream temperature

Maximum water temperatures did not exceed 15.0 °C in either spawning tributary during 2003 or 2004. Average daily water temperatures did not exceed 12.0 °C at either site. Average weekly water temperatures fell below 9.0 °C in both spawning tributaries during the period when bull trout were first observed spawning in 2003 and 2004.

Discussion

The unusual and unexpected downstream–upstream adfluvial migration patterns exhibited by Secesh River bull trout whereby fish migrated downstream from a lake to a larger river system, migrated upstream to spawning areas during spring and summer, spawned or staged, migrated downstream in the river to a tributary, and migrated upstream to a lake in the fall to over-winter (Figs 2 and 3), are in sharp contrast to typical adfluvial migrations. Typical adfluvial migrations are a series of upstream movements from a lake or reservoir to upriver spawning locations followed by a return downstream to the lake or reservoir of origin (e.g. Fraley & Shepard 1989; Howell & Buchanan 1992; Mackay et al. 1997; Brewin et al. 2001). We found only two cases of downstream–upstream spawning migrations in the literature for bull trout (Carson 2001; Hogen & Scarnecchia 2006), and one similar case for anadromous Dolly Varden (Armstrong 1974). In southeast Alaska, anadromous Dolly Varden were observed to migrate downstream to the ocean from over-wintering locations in a lake system, to feed in the ocean during summer, to then migrate upstream into an unrelated nonlake system to their natal stream to spawn, and then migrate downstream to the ocean before returning upstream in a lake system to over-winter (Armstrong 1974). Carson (2001) described a fluvial migration pattern which he observed in two fish that were captured upstream of their spawning tributary in the McCleod River, Alberta. These bull trout made subsequent downstream migrations, entered a tributary to apparently spawn and returned to their previous upstream capture location to over-winter. Similarly, Hogen & Scarnecchia (2006) observed five adfluvial migrants move downstream from the Glory Hole, a small (2 ha) flooded mine pit in the EFSFSR, Idaho enter a tributary to apparently spawn, and migrate upstream to the Glory Hole to over-winter. The Glory Hole has only been present for 60 years, suggesting that this particular migration pattern developed recently in the neighbouring EFSFSR watershed. This type of downstream–upstream migration pattern observed for bull trout was a minor component in both studies.

Loon Lake, a 60 ha high mountain lake in the Secesh River watershed (Fig. 1), is evidently of greater importance for Secesh River fish than is the Glory Hole for EFSFSR fish (Hogen & Scarnecchia 2006). Results from radio-tagged fish indicated that the utilisation of Loon Lake for over-wintering, inter-seasonal staging, and possible juvenile rearing leads to a major adfluvial component of bull trout life history in the Secesh River, whereas utilisation of the Glory Hole in the nearby EFSFSR led to only a minor adfluvial component (Hogen & Scarnecchia 2006). Over-wintering in Loon Lake by consecutive-year migrants during successive years also indicated fidelity to this habitat. This behaviour was evidenced by two consecutive-year migrants (Fig. 2), and three of four surviving in-season migrants initially captured in Loon Lake during 2004 which survived to return to the lake in the fall (Fig. 3). Fish remaining in Loon Lake through the summer did not migrate (Fig. 4) and utilised Loon Lake for inter-seasonal staging, indicative of either nonconsecutive-year migrations or juvenile rearing. Adfluvial life history strategies have also been found to be common in other watersheds in the region (e.g. the Clark Fork watershed, Dunham et al. 2001; Neraas & Spruell 2001) where streams have low productivity and lakes are important components of the watersheds. In typical high-elevation Idaho watersheds where riverine productivity is low, the adfluvial life history strategy, where possible, may be favoured by providing opportunities for more rapid growth, larger size and higher fecundity, much as anadromy functions for many other salmonids (Gross 1987; McDowall 2001).

The precise mechanisms by which adfluvial patterns of Secesh River bull trout developed are unknown. Migratory life history strategies in the charrs have been characterised as exploratory adaptations, having evolved from re-colonisation and dispersal following retreating glaciers along glacial margins where habitats were cold, unproductive and highly unpredictable (Power 2002). Colonisation and dispersal are adaptive mechanisms of exploration that favour migration as a means to opportunistically exploit available resources (Northcote 1978; Power 2002). Exploratory migrations can also help organisms maintain spatial diversity by extending their range beyond the limits of familiar spatial units, while retaining the ability to return to those familiar areas (Baker 1978). Bull trout in the Secesh River have evolved with a persistent kokanee population in Loon Lake, a relict of an anadromous sockeye population now thought to be extinct. Exploratory migrations could have mediated the development of these unusual adfluvial patterns in response to abundant food resources in Loon Lake. Olfaction is one mechanism that could explain the detection of upstream productive habitats in Loon Lake (Nordeng 1977; Näslund 1992). Further research is needed to identify the ecological mechanisms involved with the development of these migration patterns.

Fluvial migration patterns (Figs 5 and 6) closely resembled those observed by Hogen & Scarnecchia (2006) in the EFSFSR. Typical fluvial migrations are characterised by a series of upstream movements from a large river to a headwater tributary for staging or spawning, followed by a return to the large river of origin, often near the previous over-wintering location (e.g. Elle et al. 1994; McLeod & Clayton 1997; Swanberg 1997; Burrows et al. 2001; Clayton 2001; Hvenegaard & Thera 2001).

The variable life history strategies as manifested through migration patterns observed for Secesh River bull trout are similar to those of other bull trout stocks and other charrs. A wide array of bull trout life histories among stocks in different localities have been documented, including adfluvial (Fraley & Shepard 1989; Olmstead et al. 2001), fluvial (Hogen & Scarnecchia 2006), resident (Chandler et al. 2001; Nelson et al. 2002) and perhaps anadromy (Baker et al. 2003) in addition to some specialised adaptations such as outlet spawning (Herman 1997). The present study and that of Hogen & Scarnecchia (2006) indicate that such variations also exist within stocks, and can develop over short periods of time as opportunities for colonisation and improved feeding arise. Moreover, even greater variations in life history strategies have been reported for sympatric arctic charr (e.g. Thingvallavatn, Iceland: Sandlund et al. 1987; Skúlason et al. 1996; Greenland: Riget et al. 1986; western Canada: Reist 1989; Norway: Hindar & Jonsson 1993; Svalbard: Gulseth & Nilssen 2001).

The low survival rate of Secesh River bull trout with the longer lived tags, the brief (2-year) duration of the study, and the lack of observations of spawning radio-tagged fish made inferences regarding migration and spawning frequency difficult. However, nonconsecutive-year migrations predominated in this study. Only two radio-tagged females were determined to be consecutive-year migrants that utilised spawning tributaries; both of these fish over-wintered in Loon Lake. As in the stationary adfluvial migration pattern, nonconsecutive-year migrations are similar to a common stationary fluvial pattern reported by Hogen & Scarnecchia (2006). In Alberta, Canada, female bull trout tended to display a higher postspawning survival and an increased incidence of consecutive-year spawning than males (McCart 1997; Clayton 2001). McCart (1997) noted that nonconsecutive-year spawning was typical when multiple years were required to accumulate sufficient energy stores for the demands of gamete production, migration and spawning. It is likely that consecutive-year migrations are sufficiently stressful to make it a subordinate strategy to nonconsecutive-year migrations in the Secesh River. In the Kakwa River, Alberta 67% of bull trout tracked through more than two successive seasons displayed a tendency toward nonconsecutive-year spawning, while 22% displayed a variation of consecutive-year spawning with nonspawning years in the sequence of years tracked (Hvenegaard & Thera 2001).

Not all migrations observed in this study were necessarily related to spawning. Some fish between 300 and 350 mm FL, in addition to some consecutive-year migrants, did not make movements consistent with spawning migrations, but instead remained in Lake Creek or the lower reaches of spawning tributaries during the spawning period. Elle et al. (1994) observed upstream migrants between 300 and 380 mm TL that did not appear to spawn in the Rapid River, Idaho. Hogen & Scarnecchia (2006) observed nonspawning fluvial migrations for three consecutive-year migrants that did not enter spawning tributaries during their second year migrations in the EFSFSR. Burrows et al. (2001) reported nonspawning migrations in the Halfway and Peace Rivers, Alberta, and attributed these migrations as movements to feeding habitats. Several species reportedly move onto salmon spawning grounds to prey on out-migrating fry during periods of juvenile migration, or feed on eggs during the spawning season (Northcote 1978). Swanberg (1997) also observed nonspawning bull trout in the lower reaches of tributaries, downstream of known spawning areas, but associated these movements with the selection of thermal refugia near coldwater springs during periods of increasing water temperatures in the mainstem Blackfoot River, Montana. Other studies have also observed patterns of nonspawning migrations for fluvial bull trout (McLeod & Clayton 1997; Clayton 2001). Consequently, nonspawning migrations are an important component of bull trout life histories, and in the Secesh River environmental conditions may promote this strategy in response to resource availability and habitat quality.

In contrast to the unusual adfluvial migratory pattern observed for Secesh River bull trout, results of several other aspects of this study were consistent with results reported elsewhere. For example, the low incidence of prespawn mortalities (7%) and tag loss (3%) were similar to those observed in other studies (Schill et al. 1994; Swanberg 1997), as were the high (49%) overall mortality rates (Schill et al. 1994; Chandler et al. 2001; Hogen & Scarnecchia 2006). Similarly, average water temperatures in spawning tributaries during the spawning period (<9 °C) were consistent with those reported for the species. Spawning typically occurs at temperatures <9 °C (McPhail & Murray 1979; Shepard et al. 1984; Fraley & Shepard 1989), while temperatures <15 °C have been consistently recognised as the single most influential factor affecting bull trout distribution (Rieman & McIntyre 1993). The rapid emigration out of spawning tributaries observed in this study is also consistent with reported observations for bull trout. Swanberg (1997) reported that most bull trout in the Blackfoot River drainage, Montana began their downstream migration shortly after spawning was completed. Hogen & Scarnecchia (2006) reported rapid downstream migrations of up to 106.4 km in a week in the EFSFSR, and Schill et al. (1994) reported postspawning downstream migration rates of approximately 4.8 km per day in the Rapid River, Idaho.

Management implications

Results of the present study and that of Hogen & Scarnecchia (2006) demonstrate that the Secesh River and the EFSFSR are two distinct stocks (i.e. have distinct spawning habitats) even though fluvial migrants of both stocks share the same winter habitat in the lower SFSR (Fig. 1). Secondly, bull trout in the low productivity SFSR sub-basin will opportunistically use large rivers, lakes or small man-made impoundments whenever available. The variable and distinct life history strategies of bull trout in the Secesh and EFSFSR is consistent with the concept of metapopulation biology where spatially structured populations exist as an assortment of discrete local populations with connectivity among the populations that could allow for the reestablishment of local populations following extinction (Hanski 1991; Hanski & Gilpin 1997). Consequently, the spatial diversity and range of life histories observed in the SFSR sub-basin may confer the greatest potential for long-term persistence, especially in highly variable environments (Simberloff 1988; Thorpe 1994; Stowell et al. 1996). Management of bull trout in the SFSR sub-basin will require active management of a variety of habitats, including Loon Lake in the Secesh River, the Glory Hole in the EFSFSR, over-wintering and migration corridors in the larger main stem SFSR, and small spawning tributaries throughout.

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