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Distinct fluvial and adfluvial migration patterns of a relict charr, *Salvelinus confluentus*, stock in a mountainous watershed, Idaho, USA

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Abstract – Sixty-five large (>385 mm fork length) bull trout (*Salvelinus confluentus*), a threatened relict charr (Family Salmonidae), were captured in the upper East Fork South Fork Salmon River (EFSFSR), Idaho, USA and implanted with radio tags to investigate their spatial and temporal movements and distribution throughout the South Fork Salmon River (SFSR) basin and beyond. All radio-tagged fish were migratory. Most fish displayed a fluvial migration pattern. They typically overwintered in the larger rivers downriver of the EFSFSR (SFSR and the Salmon River further downstream), migrated upriver to the EFSFSR in June and further upriver into small (<2 m wide) tributaries to spawn in August and September. Both consecutive-year and nonconsecutive-year spawners were found. A typical migration distance between the overwintering habitat and the spawning habitat was 100 km. A minor fraction (<10%) of the fish displayed an adfluvial life history pattern, overwintering in a small (2 ha) 60-year-old flooded mine pit in the EFSFSR upstream of the spawning tributaries. The stock exhibited distinct site fidelity for spawning and overwintering. Similar fluvial and adfluvial migration patterns have been reported for bull trout in the region as well as for other charr species worldwide. Effective management of this and other migratory charr stocks will require protection of a wide range of habitats, from large rivers to the smallest tributaries.

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Key words: Charr; migration; adfluvial; fluvial; bull trout

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Introduction

Effective conservation of charrs (*Salvelinus* spp.) should be based on a thorough understanding of their often complex life histories and migration patterns (Rieman & McIntyre 1993). Throughout the northern hemisphere, charrs display a wide range of migration patterns, including migrations between river segments (fluvial potamodromy; Schill et al. 1994), between rivers and lakes or reservoirs (adfluvial; Stelfox 1997) and between rivers or lakes and the sea (anadromy; Johnson 1989; Berg & Berg 1993). Migrations, both upstream and downstream, are usually undertaken for spawning (Schill et al. 1994) or for improved feeding opportunities (e.g., Naslund 1992; Doucett et al. 1999; Gulseth & Nilssen 2001). The great plasticity in charr life histories (Reist 1989), including the development of diverse migration patterns (McCart 1980) and exploratory behaviours, has been suggested as being highly adaptive for energy acquisition in the habitats

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in which the species evolved: cold, unproductive, ice- and sediment-influenced, unstable waters associated with glaciation (Power 2002).

The bull trout (*Salvelinus confluentus*), a native charr of the northwestern United States and Canada, has suffered major declines in the past century, especially those relict stocks inhabiting the southern portion of its range. Several factors have contributed to the decline of the species, including overharvest, habitat disruption, non-native species competition and hybridisation with non-native brook trout (*Salvelinus fontinalis*). Management of bull trout has been complicated by several factors, including the species' patchy distribution (Rieman & McIntyre 1993), its tendency to migrate long distances and utilise widely separated habitats (Swanberg 1997) and our lack of knowledge about population (stock) identity and discreteness (Rieman & McIntyre 1993). Insufficient knowledge of the spatial and temporal distribution of individual charr stocks also makes it difficult to designate appropriate conservation areas (Stowell et al. 1996). All the above problems exist for the bull trout in the East Fork South Fork Salmon River (EFSFSR), Idaho, a southern relict stock thought to be part of a central Idaho stronghold for this threatened species (USFWS 1998). As with many charr stocks in Idaho, the Pacific Northwest, and worldwide, the distribution and migratory range of the EFSFSR bull trout stock is poorly understood. The objectives of this study were to: (i) assess spatial and temporal distribution of bull trout in the upper EFSFSR and its tributaries; and (ii) characterise individual and group bull trout movements by season. To the extent that migration patterns of bull trout in EFSFSR correlate with those of other charrs, results from and implications of this study will be useful in the management of various migratory charr stocks worldwide.

Study area

The study was located in west-central Idaho, USA within the South Fork Salmon River (SFSR) drainage. The study area has a short growing season, with most precipitation (mean 79 $cm \cdot year^{-1}$) falling as snow. Frost can occur any day of the year at elevations higher than 2133 m (Hogen 2002).

Fish sampling was centred in the upper EFSFSR watershed (area 33,994 ha). The EFSFSR flows through a forested, v-shaped canyon with mostly steep topography. EFSFSR stream channel gradients average about 4%. Geology in the SFSR is primarily granitic (Idaho batholith) with some volcanic and metamorphic material. The granitic material results in a low productivity of the streams; it also weathers into a fine substrate most common in disturbed streams (Klamt 1976; Clayton & Megahan 1997). The highest runoff period in the EFSFSR is typically in a 6-week period in May and June from snowmelt. Over the period 1929–1995, mean June discharge of the EFSFSR at Stibnite was 3.3 $m^3 \cdot s^{-1}$; mean August discharge was 0.45 $m^3 \cdot s^{-1}$ (Kuzis 1997).

Twentieth century gold-mining activities have resulted in the formation of the Glory Hole, a former mine pit and now a 2-ha body of water located 19 km upstream of the EFSFSR mouth. The Glory Hole had a maximum depth of 13.4 m in 1999, with most of the pit deeper than 6 m.

Methods

Capture

Bull trout were captured in the EFSFSR watershed (above the confluence with the SFSR) by hook and line sampling using artificial lures as well as circle hooks baited with salmon eggs. Sampling occurred almost daily from 29 June to 12 August 1999, and from 3 July to 15 August 2000. The 65 bull trout chosen to be radio tagged ranged in length from 320 to 790 mm fork length (FL) and in weight from 385 to 4390 g.

Radio tagging

Fish were implanted with coded radio tags by surgery. The tags were of three different dimensions designed to keep the tag weight below 2% of the fish's body weight (Winter 1996; Swanberg 1997). In 1999, 25 larger Lotek MCFT-3FM tags (10.3 g, 11 mm × 59 mm) and 11 smaller Lotek MCFT-3BM tags (7.7 g, 11 mm × 43 mm dimensions) were implanted. The typical life for both of these tag types was 238 days, or only a single spawning and overwintering season. In 2000, 11 intermediate-sized tags (Lotek MCFT-3EM; 8.9 g, 11 mm × 49 mm) were implanted. The estimated life of these tags was 439 days. Tags transmitted 24 $h \cdot day^{-1}$ with a 5-s burst rate.

Captured fish were held in individual stream tubes (90 cm × 15 cm or 90 cm × 10 cm) made of water-pervious (2-cm holed) PVC pipe with a sliding door at one end. On warm and sunny days, surgery was postponed until early evening.

Surgical procedures are detailed in Hogen (2002) and summarised here. All surgeries were conducted on site. Immediately prior to surgery, each fish was placed into a holding tank that contained 80–90 $mg \cdot l^{-1}$ tricaine methanesulphonate (MS-222) solution. Anaesthesia occurred in 1–2 min. Each fish was then placed on its dorsum on a padded v-shaped holder. MS-222 solution was continuously pumped over its gills and head to maintain anaesthesia throughout the surgery.

A 4-cm incision was made with a scalpel and scalpel guide anterior to the pelvic fins approximately 3 cm from the mid-ventral line on either the left or right side. A grooved receiver was inserted posteriorly through the incision, with its end positioned posteriorly to the pelvic fins. A 14-gauge needle (10-cm long) was then pushed through the skin onto the grooved receiver and then slid anterior toward the incision. The tag antenna was guided through the needle until it extruded. The needle and grooved receiver were removed from the incision and the tag was placed into the body cavity. Suturing with absorbable sutures consisted of three surgeon's knots.

After tag implantation, each fish was transported back to the stream tube to recover. Fish were held in the stream tube for a minimum of 15 min for recovery and then released at the capture site.

Radio telemetry

Movements of tagged fish were followed by fixed and mobile tracking using two Lotek SRX400 radio receivers, one fixed at a station and the other portable. The fixed receiver was located on a streambank of the SFSR 0.8 km downstream of the Secesh River confluence (Fig. 1). A six-element Yagi directional antenna was mounted on a large tree at the site. A data logger recorded the time and date when radio-tagged fish passed the site. The receiver was removed from November through mid June to avoid freezing temperatures. The portable receiver was moved primarily by truck, but also by airplane and on foot. Mobile tracking was conducted at weekly intervals from July through September, and bimonthly from October through June. During the July through September (3-month) period, each fish was contacted by either fixed or mobile tracking an average of once every 5.6 days in 1999 and once every 4.2 days in 2000. The most frequent average rate of encounter for an individual fish was once every 4.0 days in 1999 and once every 1.9 days in 2000; the least frequent rate of encounter for an individual fish was once every 8.3 days in 1999 and once every 15.2 days in 2000.

Determining the location of a fish within 50–100 m was considered adequate for the study objectives, except during spawning, when more precise locations (to within 1 m) were sought. At suspected spawning sites and times, triangulation was used to pinpoint the fish's location more accurately. Fish locations were recorded using a combination of Global Positioning System (GPS) coordinates, topographic maps or road distances from known locations. When an individual fish was not located by tracking with a truck, tracking by foot was conducted in areas without roads. If a fish was still not located, tracking by aircraft was conducted.

Attempts to observe and locate fish spawning sites were made with each contact during the fall season,

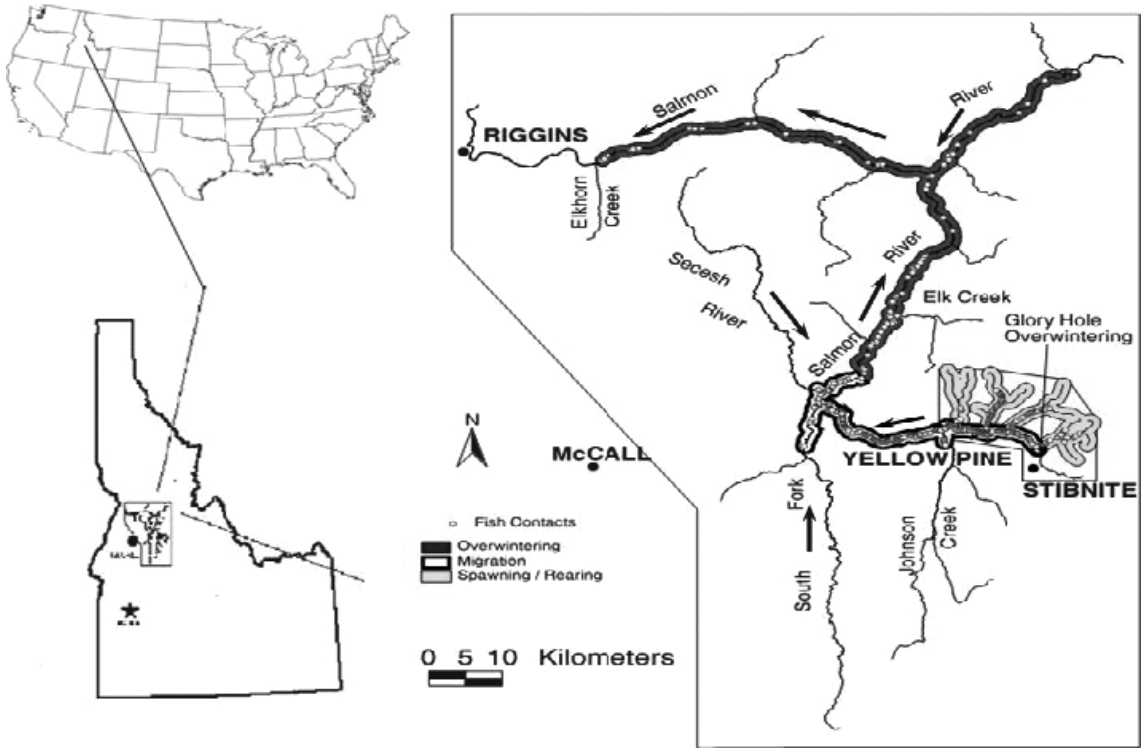

Fig. 1. Map of study area showing bull trout overwintering, migration corridors and spawning and early rearing locations determined by radio telemetry, 1999–2000. Arrows indicate direction of flows.

which was known to be the spawning period from other studies elsewhere (Shepard et al. 1984; Schill et al. 1994; Swanberg 1997). Active redd construction, pairing of fish in small headwater tributaries in the fall and the guarding of a redd were all considered to be evidence of spawning activities.

The telemetry data were quantified by river kilometre, expressed as the distance from the mouth of the Columbia River to the location of the radio-tagged fish. When upstream and downstream movements were >0.2 km between contacts, they were recorded as new locations; if no movement >0.2 km occurred, the fish was considered stationary. In the telemetry analysis, each individual fish was the experimental unit (Winter 1996). Migration was defined as the act of moving from one spatial unit (e.g., overwintering habitat or spawning habitat) to another, and changing position within a single spatial unit was defined as a movement (Baker 1978).

Analysis

All fish locations were graphed and visually inspected for patterns of individual and group movements. Patterns of movement were qualitatively categorised as migratory or nonmigratory. Migratory patterns were further described as fluvial or adfluvial.

To quantitatively test if fish movements were nondirectional or directional, a nonparametric runs test (Ramsey & Schafer 1997) was used for each individual fish and all fish were grouped together from 1999 and 2000. If the fish moved upstream from its location the previous week, it was categorised as a '+'. Downstream movement was categorised as a '−'. If a fish did not move from its location the previous week (<0.2 km), the data were disregarded. If the data were directional, a run (string of upstream or downstream values) would tend to be long and the number of different runs would tend to be small (Ramsey & Schafer 1997); this characteristic run would signify a fish migration. The null hypothesis was that a radio-tagged fish's movement was nondirectional.

The nonparametric runs test statistic (μ) was expressed as:

$$\mu = \frac{2mp}{m+p} + 1,$$

where m is the number of '−' and p the number of '+'.

The standard deviation of the number of runs (δ) was expressed as:

$$\delta = \frac{\sqrt{2mp(2mp - m - p)}}{\sqrt{(m+p)^2(m+p-1)}}.$$

The test statistic used was:

$$Z = \frac{(\text{number of runs}) - \mu + C}{\delta}$$

where C is a continuity correction. C was set at 0.5 if the number of runs was less than μ and at −0.5 if the number of runs was greater than μ.

A t-test was used to investigate if consecutive-year migrants from 1999 moved upstream in 2000 at the same rate as fish radio tagged in 2000. Weekly movement rate for each fish was considered a sample.

Seven geographic areas were delineated: Salmon River, SFSR, lower EFSFSR (mouth upstream to Johnson Creek), upper EFSFSR (Johnson Creek upstream to headwaters), tributaries to upper EFSFSR, Johnson Creek and tributaries to Johnson Creek (Fig. 1). A chi-square test was used to evaluate if there was a statistical difference ($\alpha = 0.05$) between the observed number of bull trout entering the upper EFSFSR and those entering Johnson Creek.

Results

Migrations and movements

Movements of individual fish and groups of fish were qualitatively assessed to be strongly directional migrations, even though the runs test indicated that individual fish exhibited both nondirectional (43 fish) and directional (12 fish) movements in both years. Analysis of group movements supported the qualitative assessment; fish from both 1999 and 2000 as groups exhibited directional patterns [1999: runs test, $N = 31$, $P = 0.01$ (Fig. 2a); 2000: runs test, $N = 30$, $P = 0.01$ (Fig. 2b)] considered to be migrations.

Fish tagged in 1999 and returning in 2000 migrated upstream rapidly in early July. Consecutive-year migrants moved upstream more quickly during the week of 3 July 2000 than other bull trout initially radio tagged in 2000 (d.f. = 27, $F = 13.35$, $P = 0.0011$).

Observed movements of 62 fish were classified into one of four patterns: consecutive-year fluvial, non-consecutive-year fluvial, adfluvial and down-river stationary. Three other fish were classified as having experienced tag loss or mortality.

Three fish exhibited a fluvial migration pattern with consecutive-year spawning. After initial tagging in the EFSFSR in late June or July, the fish migrated upstream to the mouth of a small tributary in early July, entered the tributary in mid-August, spawned or staged there from late August through mid-September, then rapidly emigrated downstream by mid-September into the SFSR or Salmon River, where they overwintered. This pattern was repeated beginning in late May or early June of the following year (Fig. 3a). The three fish entered the same major tributary (although not

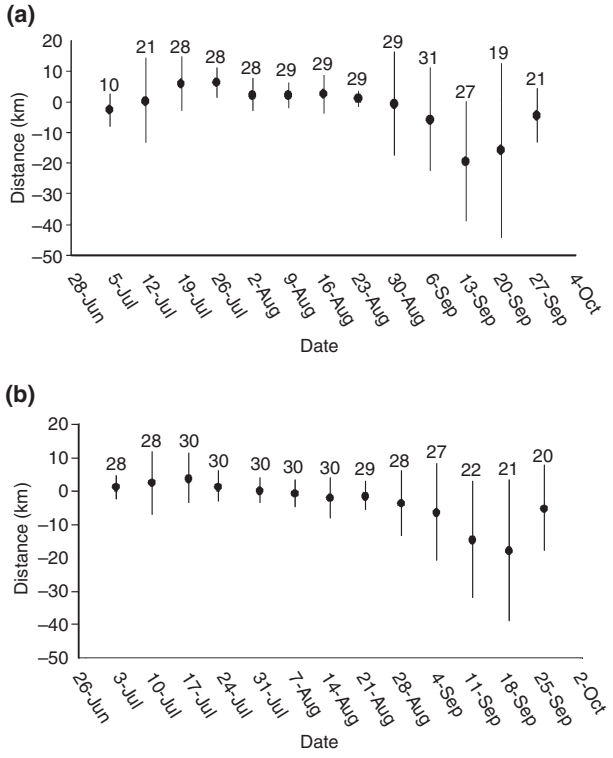

Fig. 2. (a) Bull trout weekly group mean migration rate (km·week^{-1}) from 5 July to 3 October 1999. Positive distances signify an upriver migration and negative distances signify a downstream migration. (b) Bull trout weekly group mean migration rate (km·week^{-1}) from 3 July to 25 September 2000. Positive distances signify an upriver migration and negative distances signify a downstream migration.

necessarily the same smaller, second-order tributary) in 2000 that they had entered in 1999. Two of the three fish maintained their tags into the second winter and migrated downstream to the same area they occupied in 1999.

Fourteen fish exhibited a fluvial migration pattern with nonconsecutive-year spawning. Nine of the 14 fish, which were initially tagged in the EFSFSR in 1999, migrated upstream to the mouth of a small tributary, entered the tributary in early August, spawned or staged there from late August through mid-September, then rapidly emigrated downstream into the SFSR or Salmon River, where they overwintered and remained throughout the summer of 2000 (Fig. 3b). The other five fish, after initial tagging in the EFSFSR in late June or July of either 1999 or 2000, migrated upstream in the EFSFSR but did not enter a small tributary. After the presumed spawning period, these fish moved downstream to overwinter in the SFSR or Salmon River.

For 33 other fish, the migratory pattern was fluvial, although we were unable to determine if they were consecutive-year or nonconsecutive-year spawners. Twenty-one fish initially tagged in the EFSFSR migrated upstream to the mouth of a small tributary, entered the tributary and spawned or staged there in late August through mid-September, after which their radio tags were found on streambanks or the streambed (Fig. 3c). The remaining 12 fish, which were initially tagged in the EFSFSR in 2000, migrated upstream to the mouth of a small tributary, staged there, entered the tributary in mid-August, spawned or staged there from late August through mid-September, then rapidly emigrated downstream to a large river (SFSR or Salmon River), where they overwintered (Fig. 3d). These fish were not tracked long enough to determine their spawning periodicity.

The adfluvial migration pattern (five fish) consisted of initial tagging in the Glory Hole (or nearby, <3 km downstream in the EFSFSR), downstream movement starting in late June, staging at the mouth of a small tributary in the EFSFSR by mid-August, entrance into the tributary in late August, spawning or staging in the tributary, rapid dispersal out of the tributary stream after spawning, followed by migration upstream in the EFSFSR back to the Glory Hole and residence in the Glory Hole for the winter (Fig. 3e). Only one fish completed this entire migration pattern, but four other fish completed portions of it.

The downriver-stationary pattern (seven fish) consisted of initial tagging in the EFSFSR, movement downstream immediately after tagging into the SFSR or Salmon River and residence there through the remainder of the study (Fig. 3f). Some of these fish moved upriver in the large river habitats but made no observable spawning migrations.

None of the 29 fish tagged in the EFSFSR downstream of the Johnson Creek confluence moved upstream into Johnson Creek during the two summers. Fish moved preferentially into the upper EFSFSR rather than into Johnson Creek (chi-square test, $P = 0.001$).

Prespawning activity

Bull trout first entered a small tributary to EFSFSR on 29 July 1999 and 10 July 2000. One fish that had entered a small tributary on 5 August 1999 was found downstream in the EFSFSR on 10 August 1999, but then had returned to the tributary by September 1. Similar activity was observed with a second fish in 2000. On 15 July, it entered a small tributary, exited the tributary between 27 July and 31 July, and was located again in a still smaller upstream tributary on 29 August.

Groups (five to 25) of large untagged fish (>400 mm) were observed congregating in pools near the mouth of small headwater tributaries from

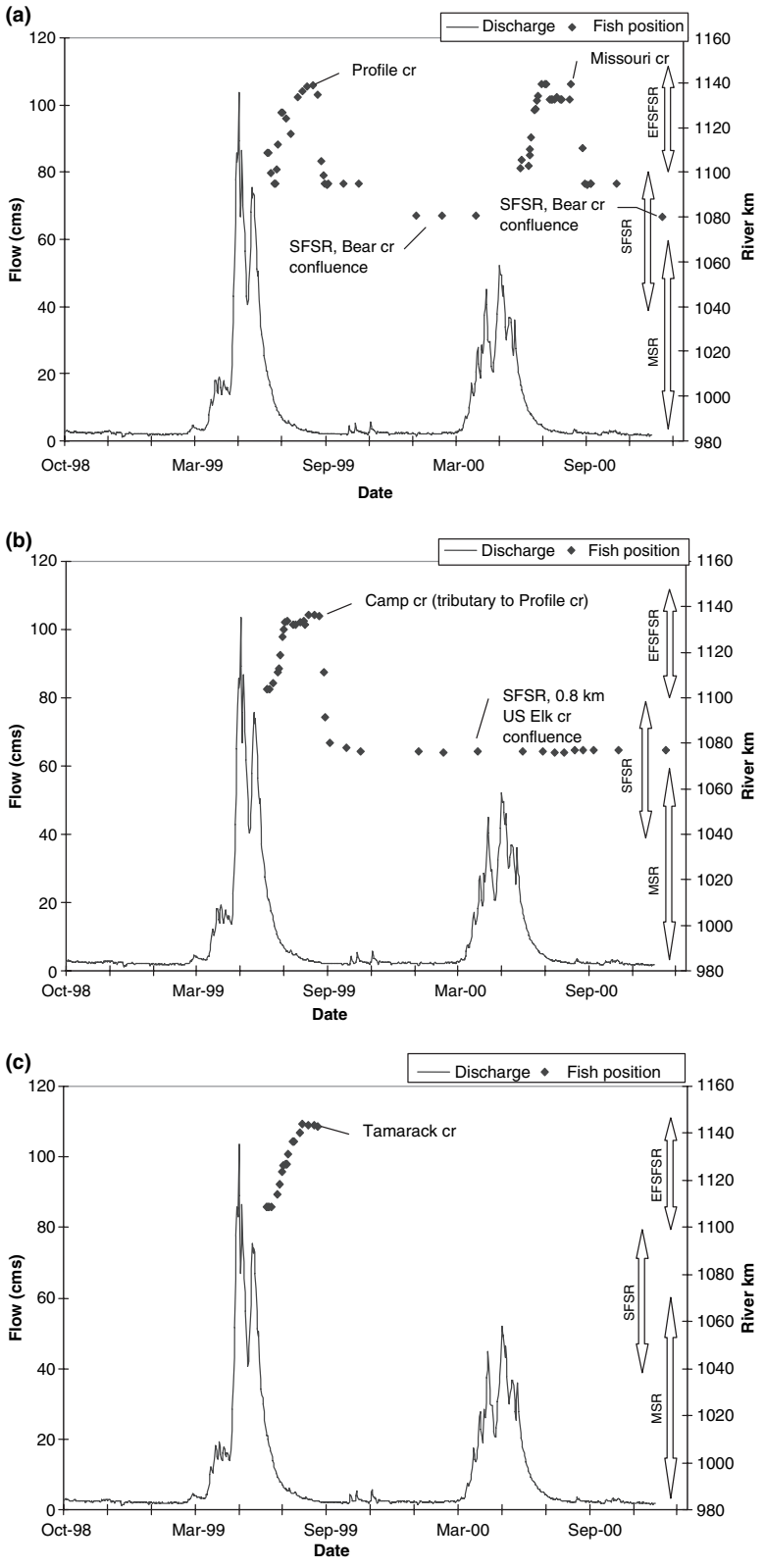

Fig. 3. (a) Bull trout W0076 fluvial migration pattern with consecutive-year spawning observed in the South Fork Salmon River subbasin, 1999–2000. (b) Bull trout W0070 fluvial migration pattern with downriver overwintering and alternate-year spawning observed in the South Fork Salmon River subbasin, 1999 and 2000. (c) Bull trout W0071 fluvial migration pattern (with probable tag expulsion after spawning) observed in the South Fork Salmon River subbasin, 1999–2000. (d) Bull trout O0010 fluvial migration pattern with downriver overwintering observed in the South Fork Salmon River subbasin, 1999–2000. Fish was tagged in 2000. (e) Bull trout W0146 adfluvial migration pattern observed in the South Fork Salmon River subbasin, 1999–2000. (f) Bull trout W0072 fluvial migration pattern (downriver-stationary) in the South Fork Salmon River subbasin, 1999–2000.

mid-July to mid-August. On 7 August 2000, nine radio-tagged fish were in one tributary of the EFSFSR but none of them had paired for spawning. Three days later, the nine fish still had not paired.

Spawning period

No radio-tagged bull trout were observed spawning during this study, so the spawning locations and

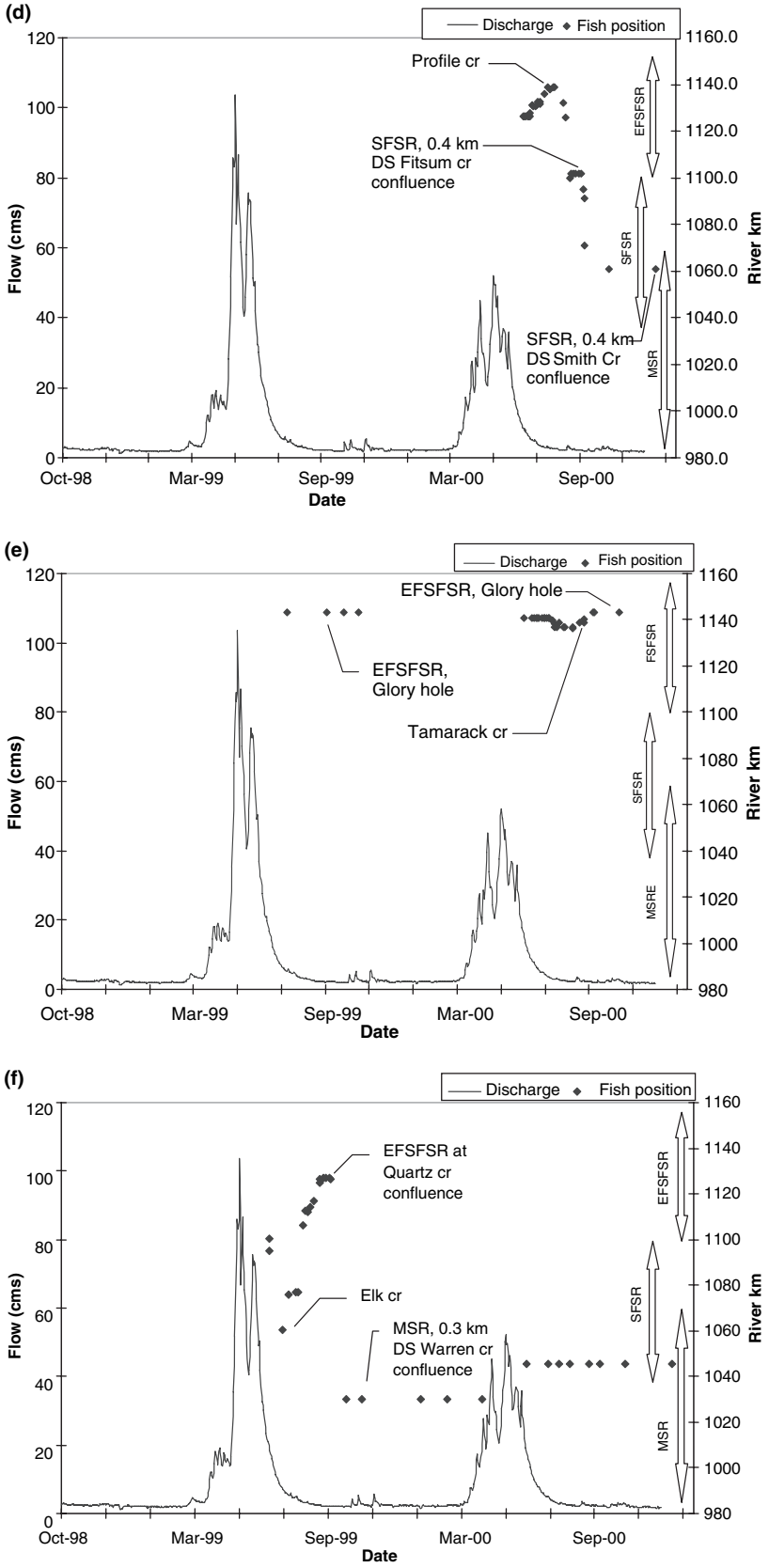

Fig. 3. Continued.

spawning period were inferred by a combination of movements of radio-tagged fish and behavioural observations of untagged fish. Prespawning movements of fish into small tributaries occurred over the period July–September in both 1999 and 2000. Contacts with 44 tagged fish were made in nine small headwater tributaries to the EFSFSR during this period. Two other fish were in the upper EFSFSR in July, August and September, but they did not enter into a tributary. Radio-tagged fish were not distributed in the same tributaries in the same proportions in 1999 and 2000. Four fish tagged in the Glory Hole also migrated downstream and entered into a small tributary during this period.

Pairing, redd construction and spawning of untagged fish were observed from mid-August to mid-September in both years. In 1999, pairing was first observed on 10 August in a tributary. Subsequent observations of pairing in tributaries occurred on 24, 25 and 31 August, and 1, 8 and 14 September. In 2000, untagged fish were first observed spawning on 28 August, with pairing and redd construction observed through 8 September.

Tag loss

Radio-tagged fish experienced high (47%) tag loss in 1999 and 2000 while in the EFSFSR headwater tributaries. In 1999, 27 bull trout entered into smaller tributaries of the EFSFSR and 12 tags (44%) were later recovered either in the tributaries or on the streambanks. In 2000, 24 bull trout entered small tributaries of the EFSFSR and 12 transmitters (50%) were recovered. None of the fish losing their tags lost them during the period soon after tagging. The average time between tagging and tag loss for those fish losing their tags was 70 days (minimum, 28 days; maximum, 351 days).

Postspawning

By 20 September of both 1999 and 2000, radio-tagged bull trout still retaining their radio tags had exited the spawning tributaries. Radio-tagged bull trout migrated downstream rapidly at this time up to 106.4 km in 1 week.

Overwintering

Fluvial bull trout overwintered in the lower SFSR and Salmon River. Of the tagged fish located during the winter, 20 were in the lower SFSR, nine were in the lower Salmon River and six were in the upper Salmon River. Bimonthly tracking during winter detected very little movement. Three fish that overwintered in 1999 migrated upstream in 2000, then returned downstream to overwinter in 2000 at the same locations (SFSR and Salmon River) as in 1999.

Discussion

Migrations and movements

The presence of several variations of fluvial migration patterns (Fig. 3a–d,f) as well as an adfluvial pattern (Fig. 3e) for the bull trout of the EFSFSR is consistent with the great plasticity of life histories and migratory patterns observed in the species elsewhere in the region (Rieman & McIntyre 1993). Except for the downriver-stationary pattern, which is difficult to interpret and may have resulted from ecological factors, stress associated with tagging or a combination of those factors, all the patterns have been described elsewhere in other bull trout stocks.

All three fluvial migrants exhibiting consecutive-year migrations into tributaries entered the same tributaries they had entered the previous year. Other studies have also documented consecutive-year spawning site fidelity (Swanberg 1997; Hvenegaard & Thera 2001). In the Kakwa River, Alberta, Hvenegaard & Thera (2001) reported that 10 of 13 (77%) bull trout displayed spawning site fidelity by returning to a specific tributary in each spawning season.

The nonconsecutive-year spawning pattern observed in this study, in which fish migrated into small tributaries to spawn, subsequently overwintered downriver in a large river and remained in the large river habitat throughout the next year, has been documented in other fluvial bull trout populations (Burrows et al. 2001; Hvenegaard & Thera 2001). In the Kakwa River, Hvenegaard & Thera (2001) reported that 18 of 27 bull trout (67%) tracked through more than two successive spawning seasons displayed a tendency towards alternate-year spawning. In our study, nonspawning consecutive-year migrants did not typically migrate upstream to the mouth of a small tributary, but instead typically remained in the lower EFSFSR or SFSR near the mouth of the Secesh River, only migrating a portion of the distance to the tributaries. In spawning years, spawners would enter small tributaries. The 18-month study period was not long enough to determine whether the pattern was alternate-year spawning, spawning at longer intervals or tag loss during the winter.

Because of the short life of some tags, early expulsion of some tags and the short study duration, we were not always able to determine if the tagged fish were consecutive-year or alternate-year spawners. In 21 cases, for example, a fish swam upstream, staged in or at the mouth of a small tributary, entered and spawned or staged in that tributary and lost its tag soon

afterward. Similar high rates of tag loss were also observed by Schill et al. (1994) and Elle et al. (1994) in Rapid River, Idaho. In the McLeod River, Alberta, Carson (2001) reported one of nine radio-tagged bull trout that entered a small tributary to spawn lost its tag either due to predation or tag expulsion. For 12 other fish tagged in 2000, the tag transmissions were adequate to demonstrate a fluvial pattern with overwintering downstream in a larger river, although the spawning periodicity was not determined. Swanberg (1997) observed a similar fluvial pattern in the Blackfoot River, Montana. In Rapid River, Elle et al. (1994) also documented fluvial bull trout that migrated upstream to a tributary, entered the tributary to spawn, emigrated rapidly after spawning and resided in the Salmon River, a large river downstream of the spawning tributary.

The adfluvial pattern observed in this study differed greatly from fluvial patterns in that fish migrated downstream out of the Glory Hole in late June to the mouth of a small tributary, apparently spawned in the small tributary and returned upriver to the Glory Hole during the winter. Adfluvial life histories are common in relict bull trout in the Pacific Northwest (Rieman & McIntyre 1993). The adfluvial pattern in EFSRSR bull trout is similar to migrations described by Fraley & Shepard (1989). In that study, adult bull trout entered tributaries from July through September, spawned during September and early October, exited the tributary after spawning and returned (downstream in this case) to the lake to overwinter. Juveniles emigrated from the tributaries into the Flathead River mainly in June and August and continued downstream until reaching Flathead Lake. Their results differed from our results in that the EFSFSR juveniles would have to swim upstream to mature in the Glory Hole and spawn downstream of their rearing area. As the Glory Hole has only been present for 60 years, this migration pattern would have had to develop over a short time period. Carson (2001) observed two bull trout perform a downstream spawning migration in the McLeod River, Alberta. These two fish were radio tagged in the river where they travelled downstream to the mouth of a tributary, entered the tributary, spawned and returned upstream to the capture site in the river. This study and the downstream migration of fish observed in the EFSFSR further raises questions about the mechanisms and cues used in identifying and locating spawning areas. Power (2002) suggested that 'olfaction, together with habitat familiarity and solar navigation, seem to be the most likely modalities involved' (p. 30) in charr homing.

The diversity of migration patterns (fluvial and adfluvial) observed in EFSFSR bull trout is similar to that observed in other charrs elsewhere (Johnson 1980; Kircheis 1980; Naslund 1990). Nordeng (1961) and McCart (1980) summarised migratory characteristics of arctic charrs (*Salvelinus alpinus*), in their regions and reported that a diversity of life history and migration patterns existed. Although anadromous life histories are common in many locations for arctic charr and are typically preferentially displayed by females over males (Mortensen & Christensen 1983), fluvial and adfluvial life histories also have been reported, especially in landlocked situations (Kircheis 1980; Reist 1989). Charrs have been characterised as having evolved migratory and exploratory life histories as adaptations favouring historical colonisation along glacial margins, areas typically characterised as cold, unproductive and unpredictable. Exploration may be adaptive as an effective colonising mechanism, and migrations may allow charrs access to better food supplies in rivers, lakes or the ocean, wherever opportunities arise (Power 2002). Growth of charrs has been shown in numerous cases to be strongly related to the productivity of the habitat (e.g., Barbour & Einarsson 1987; Rubin 1993) and fecundity (and presumably fitness) positively related to fish size (Johnson 1980). Such historical migratory and exploratory adaptations in charrs may also serve a relict charr such as EFSFSR bull trout well in its habitat. Productivity for fish in the batholith-dominated SFSR basin is low, and spawning areas in the headwaters may provide little food or overwintering habitat. In this situation, a migratory, fluvial life history may be the most adaptive life history, particularly where a lack of large lakes in the upper EFSFSR basin prevents the development of all but a modest adfluvial life history (i.e., associated with the Glory Hole; Fig. 3e).

In this study, three spatial units were identified based on the results of radio tagging: overwintering habitat, migrational corridor and spawning and early rearing habitat (Fig. 1). Overwintering habitat was in the larger rivers including the SFSR and a portion of the Salmon River. The Glory Hole was also identified as overwintering habitat for the adfluvial fish (Fig. 1). Migration corridors consisted of segments of the SFSR and the EFSFSR from its confluence with the SFSR (river km 1099.9) upstream to the Glory Hole (river km 1143.0) including Johnson Creek. Spawning and rearing habitat was in the small tributaries including several small tributaries to EFSFSR as well as headwater tributaries to those tributaries (Fig. 1). Although feeding studies were not conducted, larger migratory adults may feed opportunistically in all these habitats.

The entry of 29 radio-tagged bull trout into the upper EFSFSR, but none into Johnson Creek, indicated that the tagged fluvial bull trout preferentially

selected the upper EFSFSR over Johnson Creek (Fig. 3). The reason for the large difference in numbers of tagged fish entering the two rivers is not clear. Johnson Creek is known to contain bull trout. The Nez Perce Tribe operated an upstream passage weir (pickets 4 cm apart) from 26 June through 13 September 2000, and during that period, 17 bull trout (390–510 mm TL) were collected in the trap and placed upstream of the weir (M. Daniel, Nez Perce Tribe, McCall, Idaho, personal communication). In addition, the Nez Perce Tribe also had a downstream migrant screw-trap located on lower Johnson Creek, where they captured 55 bull trout; four of them were greater than 350 mm FL. It is possible that our sample of radio-tagged fish did not adequately include Johnson Creek fluvial bull trout. It is also possible that the migration timing of Johnson Creek fish did not coincide with when we radio tagged fish. It may also be that the fluvial bull trout population in Johnson Creek and its tributaries is small relative to that in the upper EFSFSR and tributaries.

Spawning period

The bull trout spawning observed in late August through mid September in 1999 and 2000 in tributaries was associated with maximum water temperatures of 7.4–12.8 °C. A drop in water temperature from 12 to 9–10 °C occurred in most tributaries during early September. The observed spawning time and water temperatures were similar to those observed for resident bull trout by Adams (1994) in tributaries to the Weiser River, Idaho. In the Rapid River, Idaho, Schill et al. (1994) observed fluvial bull trout spawning in late August through mid-September as water temperatures dropped from 10 to 6.5 °C. Fraley & Shepard (1989) observed adfluvial bull trout spawning when water temperatures dropped below 9 °C.

The three radio-tagged bull trout that were consecutive-year spawners returned to the same tributaries as the previous year. Swanberg (1997) observed similar consecutive-year spawning in a tributary of the Blackfoot River, Montana.

Overwintering

The observation that radio-tagged fluvial bull trout moved little during the winter months (less than 1 km) is similar to results reported elsewhere. Swanberg (1997) reported that movements during the winter were very local, never exceeding 300 m. Elle et al. (1994) also found that fluvial bull trout from the Rapid River, Idaho typically remained in one habitat unit for the overwintering period and generally moved less than 100 m between contacts. Even with the reduced tracking schedule in winter, the evidence indicates that overwintering movements were much less extensive than in other seasons.

While observing the locations of the radio-tagged bull trout in the winter, we observed the fish using large deep pools and runs and avoiding shallow riffles. This habitat use is similar to that reported by Schill et al. (1994) and Elle et al. (1994) in the Salmon River near Riggins, Idaho. In our study, three radio-tagged fluvial bull trout exhibited site fidelity to the overwintering habitat by returning to the same location as the previous year. Swanberg (1997) also observed overwintering site fidelity in three radio-tagged bull trout in the Blackfoot River, Montana. Little overlap of EFSFSR fluvial bull trout overwintering habitat was observed with the Rapid River fluvial bull trout overwintering locations (Elle et al. 1994; Schill et al. 1994), even though the two groups had free access to the same overwintering sites. Of the 63 fish tagged and subsequently contacted in overwintering habitats [38 from this study, 17 from Elle et al. 1994 and eight fish from Schill et al. (1994)], only one fish from our study and one fish from Schill et al. (1994) used the same overwintering locations. As the overwintering and spawning areas of the radio-tagged bull trout from the Rapid River and the SFSR do not overlap, it appears that they are separate stocks with not only distinct spawning areas, but also distinct overwintering areas.

Management significance of diverse migration patterns

Results of this study show that bull trout in the EFSFSR have evolved a variety of migrational patterns, both fluvial and adfluvial, similar to bull trout in the region and other charr species throughout the northern hemisphere. Fish from the EFSFSR also exhibited migration patterns consistent with the idea that several distinct stocks of bull trout exist in the SFSR basin. The highly variable life histories and migration patterns associated with this species is consistent with genetic results (Taylor et al. 1999) indicating that most of the molecular genetic variations occur at the interpopulation and inter-region (coastal vs. interior) levels. Maintenance of bull trout habitat for such a highly migratory species composed of numerous stocks will thus require actions in a variety of habitats, from the larger main stem rivers to the smallest tributaries.

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