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Seasonal timing of reproductive migrations in adfluvial bull trout: an assessment of sex, spawning experience, population density, and environmental factors

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Abstract

Using individual tags combined with a fish fence operated at the mouth of Smith-Dorrien Creek, the primary spawning habitat for Lower Kananaskis Lake bull trout, we approximated a complete census of the spawning population from 1996 to 2000 to assess whether timing of upstream and downstream spawning migrations varied with extrinsic and intrinsic factors. The timing of both upstream and downstream migrations varied with sex, previous spawning experience, density and temperature. Inferred spawning duration based on the predicted upstream and downstream migration dates indicated that experienced female spawners spent the least amount of time upstream, and first-time spawners spent the most time upstream. No consistent differences in upstream migration timing were observed between non-repetitive and repetitive spawners. We suggest that variations in spawning migration timing observed in Lower Kananaskis Lake may be linked to environmental factors that influence upstream swimming ability, and acquisition and expenditure of energy with respect to reproduction.

Introduction

Bull trout, *Salvelinus confluentus*, a coldwater fish species native to western North America, was once widely distributed throughout mountain and foothill rivers and lakes. Over the past century, bull trout populations have seen significant declines in abundance and distribution, and is presently listed as threatened in the US and as a species of concern or threatened in many regions in Canada (U.S. Fish and Wildlife Service 1999; COSEWIC 2012). Declines have been attributed to barriers to migration, habitat degradation or fragmentation, angling pressure, and competition with introduced species (COSEWIC 2012). Bull trout are a long-lived, late-maturing species that typically inhabit pristine, cold water environments, and as a result, are particularly susceptible to fishing and environmental pressures.

Bull trout exhibit a wide array of life history strategies including resident, fluvial, adfluvial and anadromous. With the exception of resident forms, spawning migrations are an important life history stage for bull trout, with populations migrating from feeding and wintering grounds in rivers, lakes or

reservoirs, and marine environments, to spawning and rearing habitat in small, cool, headwater streams (Fraley and Shepard 1989; Brenkman and Corbett 2005; Dunham et al. 2008). These annual or semi-annual spawning migrations can vary in length among populations from as little as a few kilometers to as much as 250 km (Starcevich et al. 2012; Tennant et al. 2016). As with any migratory species, understanding migration timing and behaviour are particularly important to the management and conservation of the species.

There is often a narrow time window for migration in many species (e.g., Cushing 1969). Since spawning migrations are often energetically costly, natural selection should favour traits that increase the probability of success in both migration and reproduction (Dahl et al. 2004). As such, individuals that migrate outside of an environmentally or physiologically optimal time are likely to face negative consequences, such as elevated migration and pre-spawn mortality (Cooke et al. 2004). Further, individuals that spawn outside of an optimal time may incur negative consequences for their progeny, such as exposure of eggs to suboptimal temperatures or a potential temporal mismatch between larval emergence and prey availability (e.g., Braun et al. 2013; Realis-Doyelle et al. 2016).

In general, the timing of spawning migrations is thought to be the result of genetic adaptation to prevailing environmental conditions (Hansen and Jonsson 1991; Dingle 1996). Interannual variability in this timing, however, has been attributed to environmental factors such as water temperature and water velocity (Northcote 1984; Jonsson and Ruud-Hansen 1985; Jonsson et al. 1990; Keefer et al. 2004). Environmental factors are thought to exert physical constraints on migration or influence physiological processes that result in behavioural changes related to migration timing (Jonsson et al. 1990; Whalen et al. 1999). Within populations, differences in spawning migration timing have been observed between groups of different size, age, sex, and spawning experience in a number of species, including bull trout (e.g., Niemelä et al. 2006; Howell et al. 2016). Potential drivers for observed demographic differences in spawning migration timing may be variations in physiology, such as swimming ability, condition, and stage of maturity (Swanberg 1997; Slotte 1999; Oskarsson and Taggart 2009), responses to different

chemical cues (Johnsen and Hasler 1980), and/or the role of previously learned migration routes between first-time and experienced spawners (McQuinn 1997).

The length of time spent on spawning grounds is another aspect of spawning migrations that may vary among species, populations, and demographic groups within populations, depending on physiology and animal behaviour (Jonsson et al. 1990; Fenkes et al. 2016). Spawning migrations are energetically costly, and increasing the time spent upstream can increase this cost through various mechanisms, such as increased time spent not feeding and aggressive behaviour associated with spawning (Kitano et al. 1994; Fenkes et al. 2016). More time on the spawning grounds, however, may also have associated reproductive benefits through procuring optimal spawning locations and by increasing the number of spawning opportunities (Block 1955; Fraley and Shepard 1989).

The adfluvial bull trout population in Lower Kananaskis Lake, Alberta, has been well studied in recent decades (Stelfox and Egan 1995; Stelfox 1997; Mushens 2003; Johnston et al. 2007; Johnston and Post 2009; Pinto et al. 2013). With the installation of a dam in 1955 and the resulting loss in spawning habitat, introduction of non-native fish species, and overexploitation, the spawning population was depressed to 60 spawning adults in 1992. Consequently, in 1992, fishing regulations were amended so that Smith-Dorrien Creek, the primary spawning habitat for Lower Kananaskis Lake bull trout, was closed to angling, and a zero bag limit for bull trout and a bait ban were implemented on the lake. In the decade following, the population demonstrated a remarkable recovery with a 28-fold increase in abundance (Johnston et al. 2007). As densities increased, Johnston and Post (2009) observed a delay in maturation, and an increase in frequency of skipped reproductive events in individuals with lower mass at length.

Here, we evaluated the timing of spawning migrations of the adfluvial bull trout population in Lower Kananaskis Lake, Alberta from 1996 to 2000 to assess what factors influenced the timing of both upstream and downstream migrations and the length of time spent on spawning grounds. In particular, we examined intrinsic factors such as sex, maturity, and spawning experience, and extrinsic factors such

as year, density, discharge and water temperature. Lastly, we assessed whether upstream spawning migration timing differed between those individuals that spawn in sequential years and those that skipped spawning and reproduced only in alternate years.

Methods

Study Area

Lower Kananaskis Lake (50°39'22"N, 115°08'13"W) is a 646-ha oligotrophic reservoir at 1677 m elevation located on the eastern slopes of the Rocky Mountains in Peter Lougheed Provincial Park, Alberta, Canada. Of its inlet streams, only one, Smith-Dorrien Creek, provides suitable spawning habitat for the native adfluvial bull trout population (Stelfox and Egan 1995). Smith-Dorrien Creek is characterised by a seasonal discharge pattern and temperature profile typical of Rocky Mountain streams. Discharge peaks in the spring or early summer, and declines toward base flow by late autumn, while water temperatures peak in mid to late summer. Although 18 km long, only the lower 13 km of Smith-Dorrien Creek is accessible to bull trout owing to impassable beaver dams and ephemeral surface flow in the upper reaches. Other fish species in the lake include rainbow trout (*Oncorhynchus mykiss*), native and stocked cutthroat trout (*O. clarkii lewisi*), longnose sucker (*Catostomus catostomus*), white sucker (*C. commersoni*), lake chub (*Couesius plumbeus*), brook stickleback (*Culaea inconstans*) and longnose dace (*Rhinichthys cataractae*) (Nelson 1965). Except for young-of-the-year suckers in the lower 500 m of the stream, and the occasional rainbow trout or cutthroat trout that temporarily move into the stream, bull trout are the only species present in Smith-Dorrien Creek (Mushens 2003).

Life History

Lower Kananaskis Lake bull trout are adfluvial, spending most of their life in the lake and only leaving to spawn in the autumn. Adult bull trout typically migrate up Smith-Dorrien Creek to spawn from August to September and return to the lake from September to October (Mushens 2003; Johnston 2005). The following spring, juveniles hatch in the creek and remain there for one to four years before migrating to the lake. The young bull trout then spend an additional one to five years in the lake before reaching

sexual maturity at six to nine years of age. Bull trout inhabiting the lake typically prey on benthic invertebrates, mysids, and fish, with larger individuals becoming increasingly piscivorous (Mushens et al. 2000). Bull trout are iteroparous spawners, but some individuals do not spawn in sequential years (Johnston and Post 2009).

Field Methods

The abundance and timing of migrating bull trout spawners in Smith-Dorrien Creek was determined annually from 1992 to 2002 as described in Mushens (2003), Johnston (2005) and Johnston et al (2007). For this study, a subset of the data limited to 1996 to 2000 was used because datasets were incomplete in 1994 and 2001, and data from preceding years was needed to determine whether individuals had spawned previously. A fish fence and bidirectional traps were operational at the mouth of Smith-Dorrien Creek throughout the summer and autumn, typically mid-July to mid-October. Captured fish were anaesthetized using clove oil or tricaine methanesulfonate (MS 222) and tagged with individually coded Floy tags (Floy Tags, Seattle, Washington, USA) and VI Alpha visual implant tags (Northwest Marine Technology, Shaw Island, Washington, USA). Adipose fins were also removed to identify fish as previously captured. Fish were weighed, measured for fork length and where possible, sex and maturity (i.e., green, ripe or spent) were determined. Trapped fish were released above or below the trap in relation to their direction of travel and after consideration of their reproductive state. Upstream and downstream migration dates were recorded for individuals identified by tag ID each year and used to determine whether an individual had previous spawning experience (Experienced) or not (First-time). Some individuals lingered at the mouth of the Smith-Dorrien Creek prior to proceeding on their upstream migration to spawn and were captured in the traps more than once in the same year. In such cases, the timing used was the first time and last time captured in the upstream and downstream trap, respectively. Mean daily temperature was recorded in the creek 100 m upstream of the fish fence using an Onset Optic Stowaway thermograph (Mushens 2003). Discharge was inferred using daily staff gauge

measurements and a previously established site-specific relationship between depth and discharge (Mushens 2003).

Migration Timing and Spawning Duration

Linear mixed effects models were used to relate the upstream migration date to a number of predictor variables with individual fish ID included as a random effect to account for the lack of independence among annual migration dates for any given individual (Pinheiro et al. 2000). A set of candidate predictor variables were selected a priori based on the objective of the study and variables known to influence the timing of fish spawning migrations (Northcote 1984; Jonsson and Ruud-Hansen 1985; Jonsson et al. 1990; Keefer et al. 2004; Howell et al. 2016). The fixed effects of interest were sex, previous spawning experience, maturity (i.e. green, ripe), water temperature, stream discharge, adult population density and year. Water temperature and stream discharge measurements on the date of migration could not be used in this analysis because of a high correlation with day of year. As such, cumulative degree day (CDD), defined as cumulative water temperature 4°C or greater from May 1st to July 31st of each year recorded near the trap at Smith-Dorrien Creek, was used as a proxy for water temperature. Based on observations that migration typically commenced only after Smith-Dorrien Creek discharge declined below 3.5 m³/s following spring freshet (Mushens 2003), the day of year when those conditions were met was used to represent discharge in the model. Density refers to the abundance of adult bull trout in Lower Kananaskis Lake prior to the commencement of the spawning migration (estimated by Johnston et al. 2007).

Owing to a lack of independence between some pairs of predictor variables (variance inflation factor (VIF) >5, Zuur et al. 2007), the list of candidate predictor variables was reduced so that maturity, discharge and year were discarded and their correlates (i.e. sex, CDD and density, respectively) were retained. The remaining fixed effects were sex, experience, CDD and density (VIF<1.2). To assess the influence of these fixed effects on the upstream day of migration, all combinations of the four main predictor variables were analysed. Model selection was based on Akaike's information criterion (AIC,

Hastie and Tibshirani 1990). The best model describing the main effects was then held constant so that all combinations of the following interactions could be tested: sex*experience, sex*density, sex*CDD, experience*density, and experience*CDD. All candidate models with a ΔAIC (difference in AIC between the given model and the lowest AIC) of 2 or less were considered to have equivalent support (Burnham and Anderson 1998). In the case of multiple possible models, the most parsimonious model was selected to be the focus of the results and discussion. All analyses were conducted using R (R Core Team 2016). The lme4 package was used to fit linear mixed effects models (Bates et al. 2015) and the car package was used to estimate VIF (Fox and Weisberg 2011).

Linear mixed effects models were used to test candidate models relating predictor variables to the downstream migration date. The model structure was similar to that described above with the following exceptions: 1. maturity was not considered since all fish were spent on their descent; 2. discharge was not considered because it was thought to be an unlikely factor influencing downstream movement; and 3. CDD was defined as cumulative water temperature 4°C or greater from September 1st to October 31st of each year recorded near the trap at Smith-Dorrien Creek. The predicted upstream and downstream dates based on the two separate models were then combined to estimate the number of days spent in Smith-Dorrien Creek, referred to as inferred spawning duration.

Reproductive Frequency

Spawning frequency was found to be irregular within the Lower Kananaskis Lake bull trout. Skipped spawning events were more frequent as population density increased, and were more likely to occur among individuals with lower mass at length (Johnston et al. 2007; Johnston and Post 2009). Wilcoxon rank sum tests (Zar 2010) were used to test a subset of data for differences in the upstream migration date and mass at length between individuals that spawned repetitively (repetitive spawners, R) and those that skipped the intermediate year (non-repetitive spawners, NR) over a three-year interval, determined using individual migration records. The intervals analysed in this study were 1996-1998, 1997-1999, and 1998-2000. Within a given three-year interval, the dates of upstream spawning

migration of NR versus R spawners were compared using years that both groups spawned (i.e., year 1 and year 3 of each interval). For example, for the interval 1996-1998, upstream migration date was compared during 1996 (year 1) and 1998 (year 3). In some cases, individuals were only captured in the upstream or downstream trap and so a migration date in the other direction was not recorded. These individuals were assumed to have completed a spawning migration and were retained in the dataset, but were only included in the analysis when upstream migration timing was known. As such, the number of individuals included in the year 1 and year 3 analyses of a given interval may differ. Only experienced spawners were used in this analysis given the potential effect of spawning experience on the date of upstream migration. Maturity status was limited to green females and ripe males because the majority (>90%) were in those two groups (Table 1).

Results

Daily water temperatures, averaged from 1996 to 2000, increased gradually during the early growing season, peaking in late July to early August, and then declined steadily (Fig. 1). Water temperatures recorded between June 1st and October 31st in 1996 to 2000 ranged from 0.2 to 8.7 °C, however, on average, seasonal peak temperatures ranged between 6 and 7 °C. Following the spring freshet, discharge on Smith-Dorrien Creek declined steadily. Daily discharge values between June 1st and October 20th in 1996 to 2000 varied between 0.5 and 7.1 m³/s. Daily temperature and discharge averaged from 1996 to 2000 are presented in Fig. 1 using a 5-point and 3-point smoothing function, respectively.

Migration Timing and Spawning Duration

The upstream spawning migration of Lower Kananaskis Lake bull trout averaged over the 1996 to 2000 period indicated movement between early August and early October, with the middle 50% of individuals moving upstream between August 22 and September 6 (Fig. 1). The peak in upstream movement of spawning bull trout coincided with the latter half of the peak and subsequent decline in daily water temperatures, when temperatures ranged between 5.5 and <7 °C (Fig. 1, Fig. 2). The peak in

fish migration also coincided with strongly declining discharge, with values ranging from ~ 1.5 to <2.5 m^3/s (Fig. 1, Fig. 2). It should be noted, however, that an earlier migration event was likely missed in 1998 during a breach in the trap in late July to early August. As a result, 461 individuals were only caught during the downstream migration and were not included in the analysis of upstream migration (Table 1).

Patterns in cumulative upstream and downstream migration by year (Fig. 3) indicate variability among years, and highlight the differences among the demographic groups. In general, tendencies for first-time spawners to migrate upstream earlier than experienced spawners were observed whereas sex-based differences appeared to be less consistent. The selected model describing upstream migration date included sex, spawning experience, density, and CDD as main effects, and the following interactions: sex*experience, sex*CDD, experience*density, and experience*CDD (Table 2, Table 3). The parameter estimates from this model (Table 4) were used to illustrate the upstream migration date by demographic group at intermediate CDD and population density levels (Fig. 4A), at low and high population densities (Fig. 5A), and at low and high CDDs (Fig. 6A). When density and CDD were held constant at intermediate values, the predicted upstream migration dates for male first-time spawners (MF), female first-time spawners (FF), male experienced spawners (ME) and female experienced spawners (FE) were August 22, August 22, August 31 and September 5, respectively. In general, first-time spawners moved upstream earlier in the season, whereas experienced fish migrated later in the season with males migrating first and female spawners last (Fig. 4A). Overall, the model predicted a 14 day spread in the upstream migration dates among demographic groups. Using the intermediate CDD day value of 339, the predicted upstream migration dates for MF, FF, ME and FE spawners at the lowest density were August 20, August 19, August 22 and August 27 respectively, and at the highest density were August 24, August 24, September 5 and September 9, respectively (Fig. 5A). At a higher population densities migration was delayed for all demographic groups, however, the delay was more pronounced in experienced fish (Fig. 5A). Using the intermediate density value of 1380 adults, the predicted upstream migration dates for MF, FF, ME and FE at the lowest CDD were August 23, August 23,

September 1 and September 7, respectively, and at the highest CDD to be August 21, August 18, August 27 and August 30, respectively (Fig. 6A). During years with higher CDD, migration dates of all demographic groups were predicted to occur earlier in the season, however, the change was most pronounced among experienced female spawners.

The selected model describing the downstream migration date included sex, spawning experience, density and cumulative degree day based on autumn water temperatures as main effects, and the following interactions: sex*experience, sex*density, experience*density, and experience*CDD (Table 2, Table 3). The parameter estimates from this model (Table 4) were used to illustrate the downstream migration date by demographic group at intermediate CDD and population density levels (Fig. 4B), at low and high population densities (Fig. 5B), and at low and high CDDs (Fig. 6B). When density and CDD were held constant at intermediate values, the predicted downstream migration timing indicated that all female spawners migrated early with experienced females migrating first. Among the male spawners, the first-time spawners migrated first and experienced male spawners were predicted to leave the spawning grounds last. The predicted downstream migration dates for all demographic groups spanned five days. At high population density, with autumn CDD held constant, only a small impact was observed with a delay in downstream migration date of experienced spawners (Fig. 5B). At higher autumn CDD, with population density held constant, all demographic groups migrated downstream earlier (Fig. 6B).

Combining the predicted upstream and downstream migration dates when density and CDD were held constant resulted in inferred spawning durations for MF, FF, ME and FE of 43, 41, 37 and 28 days, respectively (Fig. 4C). With CDD held constant, inferred spawning durations of MF, FF, ME and FE of 46, 45, 43 and 36 days, respectively, at low density, and 42, 39, 34, and 25 days, respectively, at high density (Fig. 5C). At high densities, spawning duration was shorter for all demographic groups, and the difference was greatest among experienced spawners. With population density held constant, inferred spawning durations of MF, FF, ME and FE of 44, 41, 37 and 27 days, respectively, at low CDD, and 38, 38, 35, and 29 days, respectively, at high CDD (Fig. 6C). CDD had the largest impact on male first-time

spawners resulting in shorter spawning durations in years with high CDD, but small and inconsistent effects on experienced spawners.

Reproductive Frequency

No consistent differences in upstream migration timing were observed between repetitive and non-repetitive spawners for males or females (Table 5, Fig. 7). Of the 12 analyses, only two comparisons were statistically significant, with repetitive male spawners migrating later than non-repetitive male spawners in 1996 (year 1 of 1996-1998 interval, Fig. 7 A1), and non-repetitive female spawners migrating later than repetitive female spawners in 1998 (year 1 of 1998-2000 interval, Fig. 7 B3). In all other cases, there was no significant difference between the upstream migration timing of the two groups, in either the year prior to or following a missed spawning event. Similarly, no consistent significant differences in upstream mass at length were observed between repetitive and non-repetitive spawners for males or females (Table 5). Of the 12 analyses, three comparisons were statistically significant, with repetitive spawners having lower mass at length in male fish in 1996 and 1998 (years 1 and 3 of 1996-1998 interval), and in females from 2000 (year 3 in 1998-2000 interval, Table 5).

Discussion

The use of individual tags combined with a fish fence operated at the mouth of the only viable spawning creek resulted in a study that approximated a complete census of the Lower Kananaskis Lake bull trout spawning population for five consecutive years. Results indicated that the timing of both upstream and downstream migrations varied with extrinsic factors (water temperature, population density) and intrinsic factors (sex, previous spawning experience). Variation in migration dates among demographic groups was higher during the upstream migration compared to the downstream migration. During upstream migration, first-time spawners migrated early and experienced female spawners migrating last, whereas downstream migration timing varied more by sex, with females returning to the lake first. Inferred spawning duration based on predicted upstream and downstream migration dates indicated that experienced female spawners spent the least amount of time upstream,

and first-time spawners spent the most amount of time upstream with shorter spawning duration occurring in high population density years. No consistent differences in upstream migration timing were observed between non-repetitive and repetitive spawners.

The upstream spawning migration peak of Lower Kananaskis Lake bull trout occurred between mid-August and early September, and aligned with peak and declining summer water temperatures and declining discharge levels. Previous studies have suggested that seasonal changes in temperature and/or discharge may trigger spawning migrations by bull trout. Bull trout spawning migrations in other populations typically occurred as water temperatures approached values between 7 and 15 °C (Fraley and Shepard 1989; Brenkman et al. 2001; Paragamian and Walters 2011; Howell et al. 2016), a range comparable with optimal temperatures for growth for bull trout (10.9-15.4°C, Selong et al. 2001). Lower Kananaskis Lake bull trout spawning migrations occurred at cooler temperatures (mean = 5.4 °C) than those observed in other populations, but at the warmest temperatures available to them in Smith-Dorrien Creek. In years with warmer environmental temperatures, upstream migrations occurred earlier, consistent with the hypothesis that bull trout spawning migrations may be initiated when temperatures approach optimal temperatures for growth for the species.

Some previous studies have demonstrated spawning migrations occurring at declining discharge levels similar to Lower Kananaskis Lake bull trout (Dolly Varden, *Salvelinus malma*, McPhail and Murray 1979; bull trout, Swanberg 1997; Starcevich et al. 2012; Howell et al. 2016), while others have noted the opposite (Brenkman et al. 2001; Tennant et al. 2016). As a correlate of temperature in Smith-Dorrien Creek, the role of discharge in migration timing cannot be discounted. Mushens (2003) observed that fish were rarely seen migrating upstream into Smith-Dorrien Creek when discharge levels were greater than 3.5 m³/s. In spring and early summer, high water velocities in Smith-Dorrien Creek are likely to act as a barrier to upstream migration (Jonsson 1991). Although changing photoperiod may act as a general cue for spawning (Wootton and Smith 2014), annual variations in the timing of upstream spawning migration for the population as a whole is more likely explained by fluctuations in temperature and/or

discharge where improved swimming ability in optimal water temperatures (Beamish 1980; Swanberg 1997) and declining discharge act together to facilitate upstream migration.

Differences in upstream migration timing based on size or previous spawning experience (largely correlated factors) have been noted previously in bull trout (Swanberg 1997; Brenkman et al. 2001; Howell et al. 2016) and other *Salvelinus* species (Dolly Varden, Oliver 1979; McPhail and Murray 1979; Kitano 1996; brook trout, *Salvelinus fontinalis*, Baril and Magnan 2002). The order of the two size peaks, however, varies among studies, with some populations comprising early-moving large/experienced spawners (Kitano 1996; Swanberg 1997; Howell et al. 2016) and others comprising early-moving small/first-time spawners (McPhail and Murray 1979; Oliver 1979; Brenkman et al. 2001). Differences based on size or previous spawning experience have been linked to discharge when larger fish migrate during higher discharge levels (Brenkman et al. 2001; Howell et al. 2016), or the role of learning migration routes when first-time spawners follow experienced spawners (McQuinn 1997). In Lower Kananaskis Lake, however, first-time spawners migrate first during higher discharge levels relative to experienced conspecifics. Consequently, neither discharge nor learned migration routes can be used to explain the observed patterns among experience groups. Differences in upstream migration timing among demographic groups have also been linked to variations in the onset or duration of maturation (Oskarsson and Taggart 2009). Dahl et al. (2004), however, found that the timing of spawning migrations in Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) were not related to ovulation date and that fish that arrived early would wait to spawn. Similarly, although Lower Kananaskis Lake first-time spawners migrated early, they remained on the spawning grounds until downstream migration dates similar to the range observed among experienced spawners. As such, early arrival of first-time spawners may be unrelated to spawning date.

The influence of sex on bull trout migration timing has not been well studied. The few studies that have assessed variation in upstream spawning migration timing in *Salvelinus* species have observed a variety of patterns (e.g., Fraley and Shepard 1989; Baril and Magnan 2002; Koizumi and Maekawa 2003).

In comparison to the influence of previous spawning experience on upstream migration timing in Lower Kananaskis Lake bull trout, sex was less important as most of the variation was associated with spawning experience. The difference between sexes, however, was greater among experienced spawners, with females migrating upstream later than males. Sex also played a more important role in determining the downstream migration timing in Lower Kananaskis Lake. Following spawning, females were found to return to the lake earlier than males, similar to previous observations in other studies (Oliver 1979; Fraley and Shepard 1989).

Based on the demographic patterns observed, coupled with the impacts of population density and temperature, we hypothesize that the main underlying driver of migration timing within this population is energy acquisition and expenditure during gonad development and spawning. For both the first and subsequent reproductive events, the final stages of gonad development occur once sufficient energy reserves are reached to meet energetic requirements for sexual reproduction (Thorpe 2007). Recovery of energy stores to levels similar to those prior to the first spawning event can be slow or incomplete in some salmonid populations (Dutil 1986; Berg et al. 1998). Consequently, individuals that spawned in the previous year may require more time to feed during the productive summer months to acquire sufficient energy before undertaking the spawning migration. A difference of 14 days was predicted between the upstream migration dates of first-time spawners and experienced female spawners (when density and CDD were held at a median value). Given the already short migration period (~2 months) in a cold, low productivity lake, an additional 14 days spent feeding during the summer productivity pulse is likely to have a noticeable impact on energy acquisition. Indeed, increased growth rate and energy acquisition has been attributed to increased consumption in related species living in environments with seasonal productivity pulses (Armstrong and Bond 2013; Sinnatamby et al. 2015). Similarly, the difference observed between sexes is most readily explained by sex-based differences in energetic costs associated with reproduction. The energy requirement for spawning female salmonids is considerably larger than that for spawning males (Sloat et al. 2014). Females invest more energy in gamete

production, show a steeper decline in condition in the months leading up to spawning, and a greater loss in specific energy content during spawning (Berg et al. 1998; Hendry and Beall 2004; Nitychoruk et al. 2013). In spawning males, energy is typically expended in development of secondary sexual characteristics (i.e., spawning colours and kype formation) and through aggressive behavior on spawning grounds to compete for and defend mates, but the energy cost is smaller (Hendry et al. 2000).

As population densities increase, individuals face increased competition for limited resources, particularly in low productivity environments (Post et al. 1999; Amundsen et al. 2007), which may be reflected in prolonged summer feeding and delayed migration. In fact, Johnston and Post (2009) noted a greater likelihood of observing a loss in mass in larger bull trout under high density conditions in Lower Kananaskis Lake. Further, the earlier upstream migration predicted at higher water temperatures may reflect increased prey availability associated with higher lake productivity in an otherwise low productivity system (Karlsson et al. 2005) and increased consumption rates (Mesa et al. 2013). Similar delays in spawning migration associated with increases in density, and advances in spawning migration associated with increased temperature were observed in Icelandic summer-spawning herring, *Culpea harengus* (Oskarsson and Taggart 2009) and Baltic cod, *Gadus morhua* (Wieland et al. 2000).

The earlier departure from spawning habitat by female spawners may also relate to the higher energy cost of maturation and spawning, and a drive to replace spent energy (Berg et al. 1998; Hendry et al. 2000; Sloat et al. 2014). The trade-off between reproductive effort and parent survival may favour an earlier departure from spawning grounds among iteroparous spawners such as bull trout, as opposed to energetically costly nest defense tactics observed in semelparous salmonids (Calow 1985; Sloat et al. 2014). On the other hand, males may benefit from remaining on spawning grounds until later by gaining the opportunity to spawn multiple times (Block 1955; Kitano 1996). That first-time male spawners do not remain on the spawning grounds as late as experienced males may reflect their lower ability to compete for mates or their relatively higher residual reproductive value (Stearns 1992). The benefit of maintaining higher fitness for expected future reproductive events may outweigh the potential gain of

multiple spawning events during their maiden spawning season. Despite the specific departure date, first-time male spawners have the longest inferred spawning duration, followed by their female counterparts, owing to their early season arrival. The energetic costs incurred by first-time spawners during their time spent upstream may, in part, explain the lower annual survivorship observed in first-time spawners in Lower Kananaskis Lake (Johnston et al. 2007).

Since energy acquisition and expenditure are hypothesized as the fundamental mechanisms underlying the observed demographic variation in Lower Kananaskis Lake spawning migrations, and skipped spawning is typical of low productivity systems (Bull and Shine 1979), the lack of consistent differences in upstream timing between repetitive and non-repetitive spawners was unexpected, specifically during the year prior to the skipped spawning event when mass at length was presumed to be lower than that of repetitive spawners (Johnston and Post 2009). Presumably, prolonged summer feeding would benefit typically lower condition non-repetitive spawners. The lack of difference in timing, however, may explain the lower survival of non-repetitive spawners (Johnston and Post 2009). The expectation that non-repetitive spawners had lower mass at length compared to repetitive spawners in the year prior to the skipped event (Johnston and Post 2009), however, was not supported in the present study. Since the individual records used in this analysis were constrained to meet specific criteria, the resulting numbers of fish included in each group in this analysis varied widely, and were at times low (range=8-197). As such, this result should be considered with caution, and warrants further study.

Despite the reduced spawning duration when densities were high, population-level fecundity increased with the number of female spawners, albeit with no impact on the number of age-1 fish (Johnston et al. 2007). Increased spawning densities likely impacted individual reproductive success as a result of increased competition for suitable spawning habitat, the impact of spawning site selection on progeny success, and greater likelihood of redd superimposition (Baxter and McPhail 1999; Mogensen and Hutchings 2012). Spawning duration, however, may have little impact on individual reproductive

success in comparison to the timing of spawning (i.e., early- vs. late-spawners). Despite the relatively short spawning duration of experienced female spawners, their reproductive success is less likely to be impacted by increased spawning densities compared to first-time female spawners owing to their ability to create deeper redds that are less likely to be disturbed by superimposition. In addition, experienced females departed from the spawning grounds later than first-time spawners during high density conditions, making disturbance by superimposition less likely.

Conducting this study on an adfluvial bull trout population occupying a simple system (i.e., a short migration to one primary spawning area) during a period of recovery from heavy exploitation facilitated a unique examination of spawning migrations. The role of temperature, and possibly discharge, in defining the general timing of upstream spawning migrations for a bull trout population, as demonstrated in this study, is consistent with much of the previous literature on bull trout spawning migrations. Conducting annual surveys of individually tagged fish, however, allowed for an in-depth assessment of demographic variation that has not previously been done for bull trout. Results suggested that differences in energy acquisition and expenditure between sexes and based on previous spawning experience can act as a driver for variations in migration timing. Although bull trout populations vary in life-history strategies and the habitats they occupy, implications of variations in energy requirements among demographic groups illustrated here, are likely to be relevant across populations. In light of anthropogenic stressors on bull trout populations, an improved understanding of the factors influencing spawning migrations may provide insight for managing and conserving a threatened species.

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618 **Figure Captions**

619 Figure 1. Smoothed mean daily water temperatures (dashed line) and discharge (solid line) measured
620 near the trap in Smith-Dorrien Creek and averaged from 1996 to 2000. Daily mean number of fish
621 captured in the upstream trap during spawning migration into Smith-Dorrien Creek between 1996 and
622 2000 (bars).

Figure 2. Frequency distribution of (A) the mean daily water temperature near the trap at Smith-Dorrien Creek and (B) the estimated discharge on the day that individual bull trout crossed the upstream trap from 1996 to 2000.

Figure 3. Timing of cumulative upstream and downstream spawning migrations by bull trout in Smith-Dorrien Creek from 1996 to 2000. Individuals were grouped based on sex, and spawning experience.

Figure 4. Predicted upstream migration date (A) and downstream migration date (B) for each demographic group: experienced male (black), first-time male (dark grey), experienced female (light grey), and first-time female (white) spawners. Predicted dates are based on parameter estimates from the selected models (Table 4) when density and CDD are held constant at intermediate values. Density was held at 1380 for both migrations, and CDD was held at 339 in Panel A and 199 in panel B. (C) Number of days spent on spawning grounds inferred from predicted upstream and downstream migration dates by demographic group at intermediate population density and CDD.

Figure 5. (A) Predicted upstream migration date vs. density, and (B) predicted downstream migration date vs. density based on parameter estimates from the selected models (Table 4) for first-time (dashed line) and experienced (solid line), male (black) and female (grey) bull trout. CDD was held constant at 339 in panel A and 199 in panel B. (C) Number of days spent on spawning grounds inferred from predicted upstream and downstream migration dates by demographic group for low population density (white) and high population density (grey).

Figure 6(A) Predicted upstream migration date vs. CDD, and (B) predicted downstream migration date vs. CDD based on parameter estimates from the selected models (Table 4) for first-time (dashed line) and experienced (solid line), male (black) and female (grey) bull trout. Density was held constant at 1380 in panels A and panel B. (C) Number of days spent on spawning grounds inferred from predicted upstream and downstream migration dates by demographic group in low CDD (white) and high CDD (grey) years.

Figure 7. Upstream spawning migration date of male (A1-A3) and female (B1-B3) bull trout that spawned in alternate years in a three-year interval (non-repetitive; NR) compared to fish that spawned repeatedly (repetitive; R) within the same three-year interval. Three intervals were assessed from 1996 to 2000. Whiskers indicate dates of 5% and 95% migrations. Grey boxplots indicate year prior to the skipped spawning event (year 1 of interval) and open boxplots indicate year following skipped spawning year (year 3 of interval). The asterisk indicates significant test results.

Draft

Table 1. (A) Number of bull trout intercepted at the upstream trap during the spawning migration into Smith-Dorrien Creek from 1996 to 2000 grouped by sex, spawning experience and maturation status. (B) Number of spent individuals intercepted in the downstream trap from 1996 to 2000 grouped by sex and spawning experience. (C) Cumulative degree day (CDD), discharge, and density for each year used in linear modelling. Discharge refers to the day of the year following spring freshet when discharge first declined below 3.5m³/s.

	1996		1997		1998		1999		2000	
A. Upstream Group Description	Green	Ripe	Green	Ripe	Green	Ripe	Green	Ripe	Green	Ripe
Male First-time	8	133	9	167	18	77	15	154	21	165
Male Experienced	0	65	1	174	24	172	6	148	10	370
Female First-time	218	2	191	1	96	2	187	0	197	0
Female Experienced	182	1	378	15	402	22	543	2	496	39
B. Downstream Group Description	Spent		Spent		Spent		Spent		Spent	
Male First-time	143		132		178		131		161	
Male Experienced	65		168		205		117		310	
Female First-time	218		157		248		139		154	
Female Experienced	182		383		452		422		485	
C. Environmental Variables										
CDD (May 1 – July 31)	331		422		482		339		313	
CDD-Autumn (Sept 1 – Oct 31)	199		258		312		194		189	
Discharge	220		193		199		233		211	
Adult Density	724		1027		1380		1631		1663	

Table 2. Top ten candidate models describing the upstream and downstream spawning migration dates of bull trout spawning in Smith-Dorrien Creek from 1996 to 2000. Independent fixed effects variables in the candidate models included sex (S), previous spawning experience (Ex), adult population density (D) and cumulative degree day (CDD). The CDD included in the upstream model comprised May 1 to July 31, and the CDD included in the downstream model comprised Sept 1 to Oct 31. Model selection was based on Akaike’s Information Criterion (AIC) and illustrated by the difference in AIC between the given model and the best model (Δ AIC). The best model is indicated by bold type.

Fixed Effects	Sex	Experience	Density	CDD	AIC	Δ AIC
<i>Upstream</i>						
	✓	✓	✓	✓	34050.49	0.0
		✓	✓	✓	34094.64	44.2
	✓	✓	✓		34399.90	349.4
		✓	✓		34447.86	397.4
	✓	✓		✓	34649.58	599.1
		✓		✓	34679.10	628.6
	✓	✓			35236.19	1185.7
		✓			35263.80	1213.3
	✓		✓	✓	35344.76	1294.3
			✓	✓	35427.33	1376.8
<i>Downstream</i>						
	✓	✓	✓	✓	30925.50	0.0
	✓	✓		✓	30945.66	20.2
	✓		✓	✓	30967.08	41.9
	✓			✓	31007.77	82.3
		✓	✓	✓	31058.88	133.4
			✓	✓	31081.20	155.7
		✓		✓	31087.57	162.1
				✓	31128.06	202.6
	✓	✓	✓		31531.18	605.7
	✓		✓		31571.81	646.3

Table 3. Top ten candidate models describing the upstream and downstream spawning migration dates of bull trout spawning in Smith-Dorrien Creek from 1996 to 2000. The main effects determined by the best model from Table 2 were held constant while all combinations of the following interactions were assessed: sex*experience (S*Ex), sex*density (S*D), sex*temperature (S*CDD), experience*density (Ex*D) and experience*temperature (Ex*CDD). Model selection was based on Akaike’s Information Criterion (AIC) and illustrated by the difference in AIC between the given model and the best model (Δ AIC). Bolded values indicate the best models based on AIC. The grey shading indicates the model that

was selected as the focus of the results and discussion and reflect the more parsimonious of the potential models.

Fixed Effects:	S+Ex+D+CDD	S*Ex	S*D	S*CDD	Ex*D	Ex*CDD	AIC	ΔAIC
<i>Upstream</i>								
	✓	✓	✓	✓	✓	✓	33733.7	0.0
	✓	✓		✓	✓	✓	33733.82	0.1
	✓	✓	✓		✓	✓	33745.62	11.9
	✓	✓		✓	✓		33747.85	14.2
	✓	✓	✓	✓	✓		33748.14	14.4
	✓	✓			✓	✓	33750.77	17.1
	✓	✓					33764.71	31.0
	✓	✓	✓		✓		33769.97	36.3
	✓		✓	✓	✓	✓	33811.81	78.1
	✓		✓		✓	✓	33817.40	83.7
<i>Downstream</i>								
	✓	✓	✓	✓	✓	✓	30878.11	0.0
	✓	✓	✓		✓	✓	30878.76	0.7
	✓	✓			✓	✓	30881.62	3.5
	✓	✓	✓		✓		30881.65	3.5
	✓	✓	✓	✓	✓		30881.82	3.7
	✓	✓		✓	✓	✓	30882.22	4.1
	✓	✓			✓		30884.64	6.5
	✓		✓	✓	✓	✓	30885.24	7.1
	✓	✓		✓	✓		30885.81	7.7
	✓		✓		✓	✓	30885.92	7.8

Table 4. Coefficient estimates, standard error (SE), and t values for the best model identified in Table 2, describing the day of year of upstream and downstream spawning migrations by bull trout in Smith-Dorrien Creek from 1996 to 2000.

Coefficient	Estimate	SE	t value
<i>Upstream</i>			
Intercept	234.59	0.302	775.8
Sex (S)	0.93	0.435	2.1
Spawning Experience (Ex)	13.35	0.348	38.3
Density (D)	1.75	0.196	8.9
CDD (May 1-July 31)	-1.80	0.264	-6.8
S*Ex	-5.22	0.524	-10.0
S*CDD	1.08	0.249	4.4
EX*D	3.42	0.266	12.9
EX*CDD	-1.16	0.288	-4.0
<i>Downstream</i>			
Intercept	274.74	0.265	1037.2
Sex (S)	2.38	0.390	6.1
Spawning Experience (Ex)	1.13	0.314	3.6
Density (D)	-0.38	0.209	-1.8
CDD (Sept 1-Oct 31)	-3.16	0.190	-16.6
S*Ex	1.51	0.499	3.0
S*D	0.56	0.251	2.2
EX*D	1.46	0.244	6.0
EX*CDD	0.54	0.245	2.2

Table 5. W statistics and p values for Wilcoxon rank sum tests comparing the day of year of upstream spawning migration and mass at length between repetitive and non-repetitive (A) male and (B) female spawners. Comparisons were conducted on the first and third year in a 3-year interval. Analyses were conducted on male and female groups separately.

Interval	Year	Upstream Migration Date		Mass at Length	
		W statistic	p value	W statistic	p value
<i>A. Male</i>					
1996-1998	1	157.0	<0.05	372.0	<0.05
	3	43.0	>0.05	64.0	<0.05
1997-1999	1	155.5	>0.05	186.0	>0.05
	3	84.5	>0.05	145.0	>0.05
1998-2000	1	478.5	>0.05	450.0	>0.05
	3	492.0	>0.05	701.0	>0.05
<i>B. Female</i>					
1996-1998	1	918.5	>0.05	113.0	>0.05
	3	593.5	>0.05	693.0	>0.05
1997-1999	1	1317.0	>0.05	1141.0	>0.05
	3	1132.0	>0.05	1510.0	>0.05
1998-2000	1	6941.5	<0.05	4580.5	>0.05
	3	6072.5	>0.05	8944.0	<0.05

Figure 1. Smoothed mean daily water temperatures (dashed line) and discharge (solid line) measured near the trap in Smith-Dorrien Creek and averaged from 1996 to 2000. Daily mean number of fish captured in the upstream trap during spawning migration into Smith-Dorrien Creek between 1996 and 2000 (bars).

247x173mm (300 x 300 DPI)

Figure 2. Frequency distribution of (A) the mean daily water temperature near the trap at Smith-Dorrien Creek and (B) the estimated discharge on the day that individual bull trout crossed the upstream trap from 1996 to 2000.

137x154mm (300 x 300 DPI)

Figure 3. Timing of cumulative upstream and downstream spawning migrations by bull trout in Smith-Dorrien Creek from 1996 to 2000. Individuals were grouped based on sex, and spawning experience.

304x381mm (300 x 300 DPI)

Figure 4. Predicted upstream migration date (A) and downstream migration date (B) for each demographic group: experienced male (black), first-time male (dark grey), experienced female (light grey), and first-time female (white) spawners. Predicted dates are based on parameter estimates from the selected models (Table 4) when density and CDD are held constant at intermediate values. Density was held at 1380 for both migrations, and CDD was held at 339 in Panel A and 199 in panel B. (C) Number of days spent on spawning grounds inferred from predicted upstream and downstream migration dates by demographic group at intermediate population density and CDD.

518x228mm (300 x 300 DPI)

Figure 5. (A) Predicted upstream migration date vs. density, and (B) predicted downstream migration date vs. density based on parameter estimates from the selected models (Table 4) for first-time (dashed line) and experienced (solid line), male (black) and female (grey) bull trout. CCD was held constant at 339 in panel A and 199 in panel B. (C) Number of days spent on spawning grounds inferred from predicted upstream and downstream migration dates by demographic group for low population density (white) and high population density (grey).

228x457mm (300 x 300 DPI)

Figure 6(A) Predicted upstream migration date vs. CDD, and (B) predicted downstream migration date vs. CDD based on parameter estimates from the selected models (Table 4) for first-time (dashed line) and experienced (solid line), male (black) and female (grey) bull trout. Density was held constant at 1380 in panels A and panel B. (C) Number of days spent on spawning grounds inferred from predicted upstream and downstream migration dates by demographic group in low CDD (white) and high CDD (grey) years.

228x457mm (300 x 300 DPI)

Figure 7. Upstream spawning migration date of male (A1-A3) and female (B1-B3) bull trout that spawned in alternate years in a three-year interval (non-repetitive; NR) compared to fish that spawned repeatedly (repetitive; R) within the same three-year interval. Three intervals were assessed from 1996 to 2000. Whiskers indicate dates of 5% and 95% migrations. Grey boxplots indicate year prior to the skipped spawning event (year 1 of interval) and open boxplots indicate year following skipped spawning year (year 3 of interval). The asterisk indicates significant test results.

304x190mm (300 x 300 DPI)