Migrating adult steelhead utilize a thermal refuge during summer periods with high water temperatures

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Anadromous fishes often use various survival tactics while migrating through main stem rivers to successfully reach spawning grounds and reproduce. Mixed-stock assemblages of anadromous adult summer steelhead *Oncorhynchus mykiss* re-enter the Columbia River from late spring through fall including the period of peak summer water temperatures, and previous studies suggest that stocks alter migratory behaviour in response to warm temperatures by seeking cool water refuges. We combined parentage-based tagging with mixed stock analyses to test whether steelhead use a non-natal tributary (Deschutes River, OR, USA) as a thermal refuge and if this migratory behaviour is associated with stock-specific run-timing. Results collected over two migration years indicated that out-of-basin fish in the Deschutes River were disproportionately from specific stocks in the Snake River (Salmon and Grande Ronde) that had migrated through the main stem Columbia River when water temperatures exceeded 21°C. Stocks migrating through the main stem river during cooler temperature periods were either less frequent (Clearwater River), or not encountered (lower Snake River) in the Deschutes River. This study facilitates an improved understanding of stock-specific migratory characteristics associated with environmental conditions in this system. Results potentially affect fisheries management, hatchery protocols, cool-water refuge maintenance, and conservation of wild Deschutes River populations.

**Keywords:** migration, mixed-stock analysis, steelhead, thermal refuge.

**Introduction**

An improved understanding of the behavioural responses and changes in distribution to temperature fluctuations is important for developing conservation and management strategies for migratory species such as marine and anadromous fishes. Anadromous Pacific salmonids ( *Oncorhynchus* spp.) typically exhibit high fidelity to their natal tributaries (philopatry), despite the large distances that they traverse throughout their lifetime (Quinn, 2005; Keefer and Caudill, 2014). However, the spectrum of natural behaviour of salmonids includes occupation in non-natal tributaries as a migration tactic to survive adverse water conditions (Goniea et al., 2006; High et al., 2006; Keefer et al., 2009). Summer-run steelhead ( *Oncorhynchus mykiss*) return to freshwater from spring through late fall, and overwinter in the main stem of the Columbia River or its tributaries for 6–10 months prior to migrating upstream to their natal areas for spawning the following spring (Burgner et al., 1992; Quinn, 2005). This protracted period for overwintering may lend itself to potentially permanent straying into non-natal tributaries, and consequential gene-flow into non-natal populations (Hand and
Olson, 2004; Carmichael and Hoffnagle, 2006; Smith and Hawkins, 2013). However, entry and residence in non-natal areas can be a temporary tactic, possibly a thermoregulatory response to warm water temperatures in main stem rivers, with eventual departure from refuges as fish continue their migration to natal tributaries (Keef er et al., 2008a, 2009).

The optimal range for many physiological processes in fishes can be exceeded at high water temperatures (Wood, 1991; Pörtner and Knust, 2007), inciting fish to seek cool water refuges (Power et al., 1999). The combination of a warming climate and lower flows through the Columbia River hydrosystem has steadily increased water temperatures (Quinn and Adams, 1996; Crozier et al., 2008). This altered thermal regime may be a factor that influences migration behaviours of steelhead and other fishes (Robards and Quinn, 2002; Keef er et al., 2004; Salinger and Anderson, 2006). Keef er et al. (2009) showed that when main stem Columbia River water temperatures were warmest (~21°C or higher) in the summer and fall, nearly 70% of radio-tagged migrating adult steelhead exited the main stem into 2–7°C cooler tributaries that drain the eastern slopes of the Cascade mountain range. Given climate forecasts for the Pacific Northwest region (Mote and Salathé, 2010), the use of non-natal streams by fish seeking thermal refuge is likely to become more common. Concurrently, the optimal thermal habitats that characterize the natal regions of some populations may shrink over time (Crozier et al., 2008; Isaak et al., 2015).

The migration of summer-run steelhead over a protracted time following re-entry into the Columbia River presents challenges in monitoring- and managing-specific stocks. Further examination of factors that may cause differential behaviour among hatchery- and natural-origin stocks, and even finer discrimination of differences among fish from particular hatcheries is warranted to be able to examine if certain protocols (e.g. juvenile rearing) may be associated with increased use of non-natal areas. Recent advances in the development of a parentage-based tagging (PBT) programme in the Snake River basin (Steele et al., 2013) allow for the stock discrimination of hatchery stocks, which comprise about two-thirds of all steelhead currently returning to the Columbia River basin annually (Fish Passage Center, Bonneville Dam adult counts; http://www.fpc.org/). Integrating PBT with mixed stock analyses (MSA) can be used to provide stock-of-origin for both hatchery- and natural-origin fish to investigate migratory characteristics of steelhead in the Columbia River. Furthermore, fixed monitoring sites throughout the Columbia River basin allow for comparisons of stock-specific characteristics during upstream migration to natal tributaries. Returning steelhead first encounter Bonneville Dam, which provides a sampling platform to estimate stock-specific abundances.

In this study, we combined PBT with MSA to test whether steelhead use a non-natal tributary (Deschutes River, OR, USA) as a thermal refuge, and if this migratory behaviour was associated with stock-specific run-timing in the Columbia River. Estimated stock proportions for fish sampled at Sherars Falls in the Deschutes River were compared with estimated stock proportions among fish sampled in the main stem Columbia River at Bonneville Dam, located ~100 km downstream. We tested the following two hypotheses regarding steelhead migration: (i) Steelhead encountered in the Deschutes River are a random sample of stocks relative to their stock-specific abundance at Bonneville Dam and (ii) relative stock proportions in the Deschutes River are coincident with migration during periods of higher main stem water temperatures in the Columbia River.

**Methods**

**Sample collections**

Adult steelhead were captured at a fish trap located at Sherars Falls on the Deschutes River (71 rkm upstream of the Columbia River confluence) during peak migration from July through October of 2011 and 2012 (Figure 1). We counted and classified steelhead into the following three categories based on fin marks: (i) natural-origin (identified via an intact or unclipped adipose fin), (ii) the local Deschutes River stock from Round Butte Hatchery (identifiable by the presence of both maxillary and adipose clips), and (iii) out-of-basin hatchery (originating from outside the Deschutes River; adipose-clipped). We estimated annual abundances of steelhead in the three categories using Petersen mark-recapture. Collection date, sex, and length were also recorded, and non-lethal fin tissues were collected from a representative sample of the adult out-of-basin hatchery and unclipped fish. Although we collected 1356 tissue samples, the final dataset for analysis included 1333 individuals. Quality control paring included the removal of hybrids (O. mykiss—Oncorhynchus clarkii), individuals with >10% missing genotypic data, and replicate samples identified by duplicate genotypes. Final sample sizes were 735 (unclipped = 283; out-of-basin hatchery = 451; unknown = 1) in 2011, and 598 (unclipped = 220; out-of-basin hatchery = 378) in 2012.

Adult steelhead sampled at Bonneville Dam (rkm 233) were composed of a mixture of multiple up-river stocks that were non-lethally sampled over 4–5 d per statistical week from April through October in 2011 and 2012 (n = 1377 and 1482, respectively). Details of the trap facility and sampling methods are described in Hess et al. (2016). Non-lethal samples from each fish included a caudal fin tissue clip for genetic analyses, and all fish were returned to the fish ladder to continue their up-river migration.

**Laboratory methods**

Genomic DNA extraction and SNP genotyping followed the methods described in Matala et al. (2014). Briefly, amplification of SNP markers was performed using Fluidigm 96.96 Dynamic Array IFCs (chips). Chips were imaged on a Fluidigm EP1™ system and analysed and scored using the Fluidigm SNP Genotyping Analysis Software. The 2011 and 2012 collections from Bonneville Dam and the 2011 collection from the Sherars Falls trap were genotyped with 180 SNP loci described in Matala et al. (2014) to perform a combination of MSA and PBT analyses detailed below. The collection from Sherars Falls in 2012 was genotyped with a subset (n = 95) of the 180 SNP loci for use in PBT analyses exclusively. This subset of 95 SNPs has been demonstrated to provide accurate parentage assignments to the PBT baseline when both parents are sampled (Steele et al., 2013).

**Parentage and reporting group assignments**

We performed parentage assignments for all steelhead sampled at both locations with 95 loci (Steele et al., 2013) and a baseline of parental genotypes from 12 steelhead hatchery stocks located in the Snake River basin (Figure 1; genotypes available at http://www.fishgen.net). The relevant parent baseline included spawn years 2008 (n = 5086), 2009 (n = 5740), and 2010 (n = 5163) in
order to assign fish that were sampled during their adult freshwater migration to spawning tributaries in 2011 and 2012. Hatchery steelhead rear for 1 year in freshwater before migrating to the ocean, where they eventually spend 1–3 years, and then return to freshwater to spawn. Here, we defined age of individuals based on the number of years spent in the ocean (1-ocean, 2-ocean, and 3-ocean ages).

Parentage analysis was performed using the program SNPPIT (Anderson, 2010; 12 August 2012 version, https://github.com/eriqande/snppit/commits/master). Assignments from SNPPIT were accepted as true parent-offspring trios if the log of odds (LOD) score met threshold criteria of LOD > 14. In pilot studies, a value of LOD < 14 occasionally failed to exclude non-parents, whereas assignments above the LOD threshold were generally consistent with available hatchery spawning records, included no same sex parent pairs, and exhibited only minor Mendelian incompatibilities (fewer than 2 mismatched loci). We set the per-allele error rate in SNPPIT at 0.5%, which was conservative compared with the observed error rate (0.2%).

The proportion of hatchery fish identified with PBT (corrected for broodstock tagging rates) and respective 95% confidence intervals (CIs) for each year at Bonneville Dam and Sherars Falls were generated using a modified version of Resampit.r (M. Ackerman, IDFG) performed in R (R Development Core Team, 2009). Additional details on methods are described in Hess et al. (2016). Briefly, individual PBT assignments were used to expand each stock proportion by its tagging rate, resulting in relative stock proportions that sum to 1.0. The “expanded” stock proportion for each PBT hatchery stock was then multiplied by the total estimated abundance derived from counts at Bonneville Dam and abundance estimates based on mark-recapture at the Sherars Falls trap (see Supplementary Table S3). Run-timing
distributions were also characterized for each PBT hatchery stock during passage at Bonneville Dam in 2011 and 2012 by multiplying the stock proportions estimated within each month stratum uniformly across daily steelhead counts for that month. We recorded the date that marked cumulative passage of 5, 25, 50, 75, and 95% of total stock-specific abundance.

For fish that did not assign to parents in the PBT baseline, we assigned stock of origin to 14 defined reporting groups (described in Hess et al., 2016; Figure 1) with 180 SNPs. This applied to the 2011 Sherars Falls collection ($n_{clipped} = 84$, $n_{uncAPPED} = 250$) and to both years for the Bonneville Dam collection ($n_{2011} = 1377$, $n_{2012} = 1482$). Reporting group proportions of monthly strata mixtures were estimated with the program GSI_sim (Anderson et al., 2008), and used to determine reporting group abundance and run-timing distributions specific to passage at Bonneville Dam for each return year. In addition, methodology for integrating PBT and MSA proportions to estimate stock-specific abundance of steelhead at Bonneville Dam is described in Hess et al. (2016), and the same methods were applied to the 2011 collection at Sherars Falls. For the 2012 collection at Sherars Falls, we estimated hatchery stock-specific abundance, because only 95 loci were available for analyses.

Differences in stock proportions and association with temperature

We compared the estimated hatchery stock proportions from PBT assignments between those estimated at the Sherars Falls trap and Bonneville Dam in 2011 and 2012 to test the null hypothesis that representation of stocks in the Deschutes River was random. Representation was considered random when 95% CIs overlapped between relative stock proportions, or alternatively, significantly non-random when differences in relative stock proportions had non-overlapping 95% CIs. To compare stock proportions among all sampled hatchery-origin steelhead, we combined the estimated abundance of the PBT assigned hatchery stocks (clipped and unclipped) with the reporting group assignments of clipped steelhead from Sherars Falls and Bonneville Dam collections. For steelhead that did not assign to PBT baselines, assignments to reporting group were compared between Sherars Falls and Bonneville Dam. We also assumed that harvest rates were relatively equal across stocks. While it is possible that harvest rates differ by stock, we expect that harvest would be similar to stock proportions that we accounted for by including stock specific abundance data from Bonneville Dam.

Temperature data for the main stem Columbia River were obtained from the water quality monitoring site at Bonneville Dam (www.cbr.washington.edu/dart/river.html). We defined 21 °C as the mean daily threshold for the high-temperature period, because this threshold has been demonstrated as the point at which more than 70% of tagged steelhead use cool-water tributaries as thermal refuge (Keefet et al., 2009). Summer steelhead begin migrating over Bonneville Dam in April with continuous passage into November. The majority of fish migrate from June to September, which generally coincides with the high-temperature period. We calculated the absolute difference in days between the high-temperature period (midpoint between the first and last day that main stem water temperature reached 21 °C) and the median date of each stock’s run timing distribution at Bonneville Dam in each year. Run-timing distributions for fish sampled at Bonneville Dam were estimated for fish assigned to PBT hatchery stocks ($n \geq 5$), and fish assigned to seven natural-origin reporting groups located upstream of the Deschutes River (Supplementary Tables S1 and S2). We used a Mantel test in the software program, PASSAGE 2 (Rosenberg and Anderson, 2011) with 9999 permutations to test the correlation between stock-specific run timing (i.e. absolute difference in days between median run timing date and high-temperature period) and stock-specific abundances estimated at Sherars Falls in relation to Bonneville Dam. Based on prior information (Keefet et al., 2009), we predicted that stocks whose peak run timing was coincident with the high-temperature period would occur at relatively higher proportions in the Deschutes River than stocks with median run-timing outside the high-temperature window.

Results

Parentage and reporting group assignments

Parentage analyses provided assignment for hatchery-origin steelhead detected at Sherars Falls, and overall, 89% (2011) and 94% (2012) of out-of-basin steelhead originated from Snake River basin hatcheries (Supplementary Tables S2 and S3; Figure 1). The remaining fish in this category were from unknown hatchery programmes in the Columbia River or unsampled broodstock parents. Specifically, 74.0% (2011) and 82.7% (2012) of out-of-basin steelhead originated from hatchery stocks in the Salmon River region with the largest representation from Pahsimeroi Hatchery, Sawtooth Hatchery, EF Salmon, and Oxbow Hatchery (Figure 2; Supplementary Table S2). The latter hatchery is located in the Snake River (Figure 1), but is included here with Salmon River stocks because of shared ancestral origin and shared MSA reporting group. Abundance estimates for each PBT hatchery stock showed the total number of Snake River hatchery fish present in the Deschutes River exceeded or was nearly equivalent to the numbers of fish from the local Round Butte Hatchery. Snake River PBT hatchery stocks were 5445 and 4603 compared with Round Butte Hatchery stock, 4063 and 4903 in 2011 and 2012, respectively (Supplementary Table S3a).

For steelhead that did not assign with parentage analyses, stock of origin was assigned to reporting groups for 249 unclipped steelhead (presumably natural-origin), 84 out-of-basin hatchery-origin, and 1 unknown fish. The total estimated abundance of the hatchery-origin stocks present in the Deschutes River was 10094 (Supplementary Table S3) with the largest representation from two reporting groups, mid-Columbia/lower Snake (MGILCS, 52.9%) and upper Salmon River (UPSLAM, 40.9%; Supplementary Table S1a). The MGILCS reporting group includes Snake River hatchery stocks (Supplementary Table S2), but also the local Deschutes River stock from Round Butte Hatchery. The stock proportions of unclipped natural-origin steelhead in the Deschutes River were represented predominantly by MGILCS (85.6%) followed by UPSALM (11.0%; Supplementary Table S1b).

Differences in stock proportions and association with temperature

Stocks with higher than expected proportions in the Deschutes River in 2011 and 2012 included all four stocks in the Salmon River region and the WALL stock (Figure 3a; Supplementary Table S2). The DWOR and CGRW stocks were found in smaller than expected proportions in the Deschutes River. Although the
Lower Snake River hatchery stocks comprised 12.7% of the abundance among PBT hatchery stocks at Bonneville Dam, they were not detected at Sherars Falls (Figure 3a; Supplementary Table S2). For the 2011 estimates of hatchery-origin fish, the combined stock abundances by reporting group demonstrated similar patterns in stock proportions as the PBT-only estimates. Specifically, the abundance of SFCLWR (DWOR and UPSB PBT stocks) was in smaller proportion, and the UPSALM (PAHH, SAWT, OXBO and EFSW) was in larger proportion at Sherars Falls relative to their respective proportions at Bonneville Dam.

For the natural-origin fish in return year 2011, there were differences between Sherars Falls and Bonneville Dam sites in terms of the relative MSA assigned proportions to out-of-basin reporting groups excluding the MGI LCS proportion. The MFSALM and UPSALM stocks were found in larger relative proportion at Sherars Falls and all other reporting groups were found in smaller relative proportion compared with Bonneville Dam estimates. Only the natural-origin UPSALM stock proportion at Sherars Falls was significantly larger with non-overlapping CIs, which had also been found in relatively high abundance among the hatchery-origin PBT stock proportions such as PAHH, SAWT, OXBO, and EFSW (Figure 3b).

Occurrence of out-of-basin stocks in the Deschutes River was associated with high temperatures in the main stem Columbia River. Mean daily water temperatures in the main stem Columbia River reached 21°C on the 4 and 5 August in 2011 and 2012, respectively, and temperatures remained at or above 21°C until the 26th and 11th of September, respectively (Figure 4). In general, out-of-basin PBT hatchery stocks with run-timing peaks coincident with the high-temperature period also occurred in relatively large proportions at Sherars Falls in the Deschutes River compared with estimated abundances at Bonneville Dam. In both years, DWOR had the latest return timing among PBT stocks, which occurred after the high-temperature period (Figure 4). Abundance estimates of DWOR at Sherars Falls were also low (0.76–2.08%) relative to the total estimated abundance at Bonneville Dam (Supplementary Table S2). The Lyons Ferry stock (LYON) had the earliest run-timing peak at Bonneville Dam, with a median run timing date that preceded the high-temperature period in both years and no fish sampled at Sherars Falls were assigned to Lyons Ferry Hatchery. The PBT stocks from the Salmon River region (SAWT, PAHH, EFSW, OXBO) and the WALL stock from the Grande Ronde River all had median run-timing dates that coincided with the high temperature period, and they were estimated to have relatively high abundance at Sherars Falls that averaged 5.15% of Bonneville Dam estimates (Supplementary Table S2). We observed a positive correlation between run-timing coincident with high-temperature period and estimated stock abundances at Sherars Falls in relation to total estimated abundance at Bonneville Dam that was statistically significant in 2012 ($r = 0.298$, $p = 0.015$; Figure 5) but not in 2011 ($r = 0.030$, $p = 0.814$).

The three natural-origin stocks from out-of-basin detected at Sherars Falls in 2011 with abundance estimates greater than zero were found to have median run-timing dates at Bonneville Dam that occurred either before (MGILCS and UPSALM) or during (MFSALM) the high-temperature period (Figure 4). Although the SFCLWR, UPCLWR, and SFCLWR groups had a median return date within the 21°C period, none of these natural-origin stocks was detected at Sherars Falls. For natural-origin stocks, there was no significant relationship between relative abundance at Sherars Falls and run-timing coincident with the high-temperature period.

**Discussion**

This study provides evidence that specific stocks of steelhead use thermal refuges to avoid prolonged exposure to high water temperatures during spawning migrations. In the Deschutes River basin, our results showed that steelhead encountered at Sherars Falls during the summer migration period were composed of relatively equal numbers of local and out-of-basin hatchery stocks. Nearly 90% of out-of-basin hatchery steelhead originated from locations over 200 rkm upstream in the Snake River (the largest tributary of the Columbia River), primarily from hatcheries located in the Salmon River (Idaho), followed by the Grande Ronde (northeast Oregon), and Clearwater (Idaho) rivers. Among the out-of-basin hatchery steelhead, the predominance of steelhead originating from Snake River hatcheries was not unexpected as an average of 82% of all steelhead hatchery production in the interior Columbia River occurs in the Snake River (available at http://www.fpc.org). In addition to hatchery-origin steelhead, specific
Figure 3. Stock proportion comparisons between Deschutes River (black bars) and Bonneville Dam (grey bars) for (a) PBT hatchery stocks in 2011 (top panel) and 2012 (bottom panel), and (b) MSA reporting groups in the 2011 return year for all hatchery-origin (clipped and PBT groups; top panel) and natural-origin (unclipped; bottom panel) steelhead. Stock proportions are based on abundance estimates of the PBT hatchery stocks (see Supplementary Table S2) and MSA reporting groups for ages combined (see Supplementary Table S1), and associated 95% confidence intervals (CIs). An asterisk represents a significant difference (no overlap in 95% CIs) in the stock proportion between Bonneville Dam and the Sherars Falls trap in the Deschutes River.
stocks of natural-origin fish from the Snake River such as UPSALM were also found to be significantly more abundant than expected in the Deschutes River and indicate that thermal refuge migration tactics are common for this stock. Our results combined with information on stock-specific run timing, corroborate other studies that suggest that specific stocks may differentially enter the Deschutes River in response to thermal stress (e.g. High et al., 2006; Keefer et al., 2009) in contrast to overwintering behaviour that is characteristic of interior Columbia basin summer steelhead in general (Keefer et al., 2008a,b).

Run-timing at Bonneville Dam was a predictor of each stock’s abundance estimate at Sherars Falls in the Deschutes River and suggests that specific stocks were forced to take thermal refuge in tributaries during periods of high water temperature in the main stem Columbia River. We observed a relatively small proportion of stocks using the cool water refuge of the Deschutes River during early- and late-migration timing through the main stem Columbia River when temperatures were less than 21 °C. In contrast, stocks from the Salmon and Grande Ronde rivers that generally migrated through the Columbia River in mid-August when mean main stem temperatures reached ~21 °C were found in high proportion in cooler waters of the Deschutes River. In general, we observed the same pattern for the 2011 return year; however, the correlation in the relationship between stock-specific migration timing and the proportion of individuals encountered at Sherars Falls was not significant. This may be because of missing parent assignments as the PBT database was initiated in 2008 and some broodstock fish were not included. For example, the Lower Snake and Wallowa parent broodstocks were not sampled in 2008, tagging rates were <95% for some Snake River hatcheries in the initial years of the PBT programme, and sampled 3-ocean age steelhead (brood-year 2007) would be progeny of broodstocks pre-dating the initiation of the PBT programme.

Steelhead typically have high philopatry to natal areas with moderate levels of dispersal to nearby populations (Quinn, 2005) and many fish may only temporarily use tributaries as thermal refuges. Previous studies show that the majority of out-of-basin steelhead use the lower reaches below Sherars Falls of the Deschutes River as a temporary refuge and eventually re-enter the Columbia River to continue their migrations (Keefer et al., 2008a, 2009). However, High et al. (2006) observed that nearly half of out-of-basin fish entering the Deschutes River were detected 71 rkm upstream at Sherars Falls and may have attempted to spawn with local fish. Whether the individuals in our study that were detected at Sherars Falls remained in the river to contribute to natural production is uncertain, but other studies have confirmed the presence of out-of-basin steelhead in tributaries during time periods of active spawning (Hand and Olson, 2004; Carmichael and Hoffmagne, 2006; Smith and Hawkins, 2013). The extent to which out-of-basin steelhead reproduce and influence the productivity of the natural-origin population in the Deschutes River warrants further study, including tests of relative reproductive success (Wilson et al., 2014).

While the results of our study support the association between stock-specific migration timing and use of the Deschutes River as a cool-water refuge, there may be other factors that influence the rate at which particular stocks are encountered in non-natal tributaries. These include broodstock source, juvenile rearing, and release strategies for hatchery-origin fish. For example,
factors related to rearing conditions may explain why specific hatchery stocks in the Snake River basin such as Pahsimeroi, Oxbow, and Sawtooth represented the largest proportion of out-of-basin steelhead encountered at Sherars Falls. Broodstock are collected and spawned at each respective hatchery, but juveniles from these programmes are transported multiple times for rearing at offsite locations and again for release in natal subbasins (USFWS, 2011). Previous studies demonstrated that juveniles transferred from rearing locations for release elsewhere, stray into non-natal tributaries at higher rates than those released directly from their original rearing facilities (Clarke et al., 2010; Dittman et al., 2010). Moreover, capture and downstream barging of juveniles may negatively affect their subsequent homing orientation along the adult return migration route and therefore lead to increased numbers of individuals encountered in non-natal tributaries (Keefer et al., 2008b; Marsh et al., 2012). Therefore, in addition to migration-timing, the complex rearing history of particular hatchery stocks may have influenced their use of a non-natal tributary during migration and warrant further investigation.

Overall, this study demonstrates that specific steelhead stocks migrating through the main stem Columbia River during periods with warm water temperature may use thermal refuges during upstream migration. These migratory patterns were identified with greater resolution than has been previously demonstrated (Keefer et al., 2009) because of the application of genetic MSA. Further monitoring of stock specific migratory behaviour may help reveal how marine, freshwater, and anadromous fishes respond to adverse water conditions such as high temperatures (Lassard and Hayes, 2003), reduced flow (Ficke et al., 2007), pollution (Williams and Oleksiak, 2008), or ocean acidification (Fabry et al., 2008).

Supplementary data
Supplementary material is available at the ICESJMS online version of the manuscript.

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