

Spatio-temporal variability in movement, age, and growth of mountain whitefish (*Prosopium williamsoni*) in a river network based upon PIT tagging and otolith chemistry

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Abstract: Connectivity of river networks and the movements among habitats can be critical for the life history of many fish species, and understanding of the patterns of movement is central to managing populations, communities, and the landscapes they use. We combined passive integrated transponder tagging over 4 years and strontium isotopes in otoliths to demonstrate that 25% of the mountain whitefish (*Prosopium williamsoni*) sampled moved between the Methow and Columbia rivers, Washington, USA. Seasonal migrations downstream from the Methow River to the Columbia River to overwinter occurred in autumn and upstream movements in the spring. We observed migration was common during the first year of life, with migrants being larger than nonmigrants. However, growth between migrants and nonmigrants was similar. Water temperature was positively related to the proportion of migrants and negatively related to the timing of migration, but neither was related to discharge. The broad spatio-temporal movements we observed suggest mountain whitefish, and likely other nonanadromous fish, require distant habitats and also suggests that management and conservation strategies to keep connectivity of large river networks are imperative.

Résumé : La connectivité des réseaux hydrographiques et les déplacements entre habitats peuvent revêtir une importance capitale pour le cycle biologique de nombreuses espèces de poissons, la compréhension des motifs de déplacement constituant donc un aspect central de la gestion des populations et des communautés, ainsi que des paysages utilisés par ces dernières. L'intégration de données de radio-étiquettes passives intégrées recueillies sur 4 ans et de données d'isotopes de strontium d'otolithes permet de démontrer que 25 % des ménominis de montagnes (*Prosopium williamsoni*) échantillonnés se déplaçaient entre la rivière Methow et le fleuve Columbia (État de Washington, États-Unis). Des avalaisons saisonnières de la rivière Methow vers le fleuve Columbia pour y passer l'hiver se produisaient en automne, et des montaisons, au printemps. Nous avons observé que la migration était répandue durant la première année de vie, les individus migrateurs étant plus grands que les autres. Ces deux groupes présentaient toutefois des taux de croissance semblables. La température de l'eau était positivement corrélée à la proportion d'individus migrateurs et négativement corrélée au moment de la migration, aucune de ces variables n'étant toutefois corrélée au débit. Les grands déplacements spatiotemporels observés portent à croire que le ménomini de montagnes et, vraisemblablement, d'autres poissons non anadromes ont besoin d'habitats éloignés les uns des autres et qu'il est donc impératif d'adopter des stratégies de gestion et de conservation visant à préserver la connectivité des grands réseaux hydrographiques. [Traduit par la Rédaction]

Introduction

Variation in movement behavior can occur among individual fish in a population (Jonsson and Jonsson 1993; Chapman et al. 2012), ranging from short movements (<100 m) whereby a fish never leaves its natal stream to more extensive movements (multiple kilometres) to larger water bodies (e.g., mainstem river). This difference in individual behavior may be linked to their response to environmental conditions and (or) characteristics of the individual. For example, seasonal migrations of tens to hundreds of kilometres made by many salmonids have been linked to water temperature and discharge (Gowan and Fausch 1996; Clarke et al. 2007; Young 2011), as well as the opportunity to overwinter in sites that may have more suitable resources (e.g., food, temperature) for the metabolic demand of the migrants (Beauchamp 2009). Alternatively, though not mutually exclusive, larger individuals may be more likely to move because food resources are not adequate to sustain their metabolic demand (Olsson et al. 2006;

Al-Chokhachy and Budy 2008; Monnot et al. 2008). Regardless of the mechanism, fish that move to more productive habitats may grow faster and may be larger than similarly aged conspecifics (Hilderbrand and Kershner 2004; Young 2011).

Mountain whitefish (*Prosopium williamsoni*) are broadly distributed and often the most abundant salmonid in western North American rivers (Northcote and Ennis 1994), yet relatively little is known about their life history and movement patterns when compared with other salmonids. Seasonal migrations of up to 95 km to spawning or overwintering habitats have been observed (Pettit and Wallace 1975; Baxter 2002), and mixtures of resident and migratory individuals have been documented (Davies and Thompson 1976; Baxter 2002). However, details such as the proportion migrating, age at first migration, and the frequency of lifetime migrations are largely unknown. Thus, there is a need to fill these knowledge gaps.

In addition, the biotic and abiotic factors influencing movement behavior of mountain whitefish and the potential consequences

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(i.e., growth, size-at-age) of migration are lacking. In previous studies (Pettit and Wallace 1975; Meyer et al. 2009; Lance and Baxter 2011), mountain whitefish in larger rivers at lower elevation had faster growth and higher rates of production, were larger size-at-age, and had greater fecundity than those in smaller rivers at higher elevation, perhaps owing to increased water temperature or food availability downstream. For example, in the upper Snake River basin, Idaho, mountain whitefish in larger rivers (stream order = 5–7) had greater growth, fecundity, and survival than those occupying smaller rivers (stream order = 2–4; Meyer et al. 2009). Thus, we hypothesized that mountain whitefish that migrate downstream to overwinter would experience faster growth rates and obtain larger sizes compared with similarly aged nonmigrating counterparts.

Because mountain whitefish are dispersed over multiple kilometres of mainstem rivers and their abundance varies across seasons (Davies and Thompson 1976; Baxter 2002; Lance and Baxter 2011), it is difficult to study their life history and migratory behavior (Fausch et al. 2002). Passive integrated transponder (PIT) tag technology and isotopic signatures in otoliths can be combined to characterize movement across a range of spatial and temporal scales. PIT tagging is a common approach to track individuals over time by providing a record of when a fish moves past a location and direction of movement, typically monitored with passive antennas (Zydlewski et al. 2006). However, detection at the antennas is not 100% efficient and does not provide information on the origin or destination of a fish. Recently, geochemical signatures in the otoliths of fish have been used to identify life history patterns of nonanadromous fish (Wells et al. 2003; Muhlfeld et al. 2012). Otolith growth is continuous and allows a retrospective analysis of age and growth via daily and annual rings, as well as an environmental history of fish (Campana and Thorrold 2001). This makes analysis of otolith chemistry particularly useful for studying fish movement and eliminates the need to mark or recapture fish, which can be logistically challenging and expensive. Unfortunately, to use otoliths to retrospectively identify life history patterns, the fish must be sacrificed. Moreover, chemical signatures in otoliths require that isotopes differ among water bodies in which the fish reside. Regardless of the limitations of each approach individually, combined they provide complementary tools to understand life history patterns of fish populations, but have been rarely used together (but see Brenkman et al. 2007; Honda et al. 2012).

The primary objective of this study was to investigate the life history patterns exhibited by mountain whitefish throughout a large river network by using PIT tag technology over 4 years coupled with otolith analyses. We focused our study on their movements between the upper Columbia River and one of its tributaries, the Methow River (Fig. 1). Specifically, our objectives were to (i) determine the extent of seasonal movements of mountain whitefish between the Methow and Columbia rivers, (ii) determine the ages and sizes at migration, (iii) assess the extent of repeat migrations, (iv) assess the duration of residence time in the Columbia River, (v) compare the relative growth of migrants versus nonmigrants, and (vi) assess whether migrations are a function of individual fish size, water temperature, and (or) discharge.

Materials and methods

The Methow River is located in north-central Washington and drains approximately 4662 km² north to south through the northern Cascade Mountains into the Columbia River. The catchment includes three major tributaries, the upper Methow River (confluence at river kilometer (rkm) 80), Chewuch River (rkm 80), and Twisp River (rkm 66; Fig. 1). Mean discharge of the Methow River was $43.8 \pm 2.2 \text{ m}^3 \cdot \text{s}^{-1}$ (\pm SE; downloaded at <http://waterdata.usgs.gov>, site No. 12449950, Methow River near Pateros, Washington, from

1959 to 2010). Annual high flows are largely associated with snowmelt, which generally occurs in May and June.

The Columbia River is highly regulated with nine dams between the confluence with the Methow River and the Pacific Ocean. The section of the Columbia River where the Methow River enters is impacted by Chief Joseph Dam upstream and Wells Dam downstream. The mean discharge of the Columbia River was $25\,177 \pm 85 \text{ m}^3 \cdot \text{s}^{-1}$ (\pm SE; measured at the inflow of Wells Dam from 1968 to 2010; downloaded at <http://www.cbr.washington.edu/dart>). Geological differences between the Methow River basin (metamorphic rocks of marine and nonmarine origin from the Mesozoic era) and the upper Columbia River basin (older sedimentary and metamorphic rock from the Paleozoic and Precambrian eras; Lasmanis 1991) provide an opportunity to distinguish isotopic signatures of strontium in their waters (Wadleigh et al. 1985; Singleton et al. 2006) such that otoliths may be used to document migration history of mountain whitefish, as has been done with Chinook salmon (*Oncorhynchus tshawytscha*) in this region (Barnett-Johnson et al. 2010; Miller et al. 2011).

In addition to mountain whitefish, other primary fish species present in the mainstem Methow River and Columbia River include Chinook salmon, coho salmon (*Oncorhynchus kisutch*), rainbow trout–steelhead (*Oncorhynchus mykiss*), bull trout (*Salvelinus confluentus*), cutthroat trout (*Oncorhynchus clarkii*), longnose dace (*Rhinichthys cataractae*), bridgelip sucker (*Catostomus columbianus*), and several sculpin species (*Cottus* spp.). Mountain whitefish in the Methow River occur at densities that are over 4.5 times that of other fish in the river, with the exception of sculpin (Bellmore et al. 2013), and their numbers may fluctuate seasonally based upon snorkel surveys (P.J. Connolly, unpublished data).

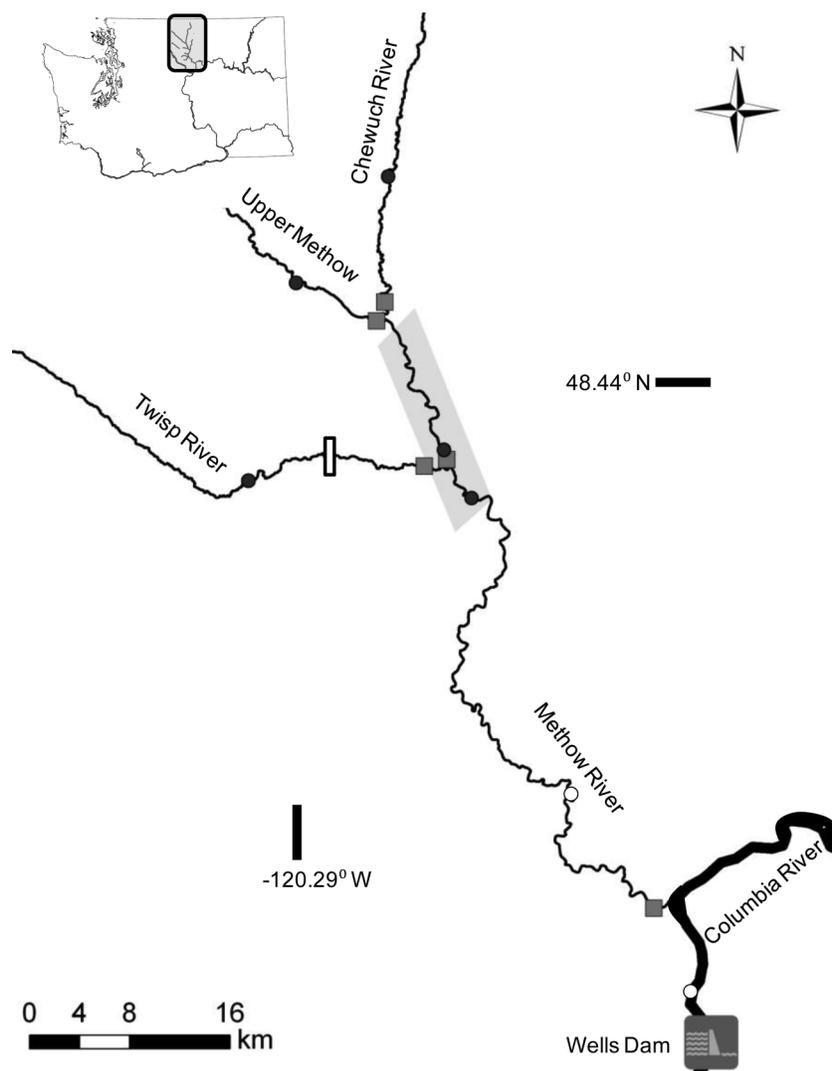
PIT tag

We captured 915 mountain whitefish using three methods. First, our main method for capturing mountain whitefish was to float gill nets (2.5–8.9 cm mesh size) downstream held by snorkelers, who would herd fish into the net. Gill netting was conducted in large pools within rkm 54 to 94 of the mainstem Methow River during early spring (March, 2009–2012) and autumn (August–October, 2009–2011; Fig. 1). Second, in the Twisp River, mountain whitefish were incidentally collected at a weir designed for capturing anadromous salmonids moving upstream to spawning areas (operated by Washington Department of Fish and Wildlife; C. Snow, Twisp, Washington, personal communication, 2012). Third, mountain whitefish were occasionally collected from two rotary screw traps located at the mouth of the Chewuch and Twisp rivers. All fish captured were measured in length (mm) and mass (g), had scales collected, and were injected with a PIT tag (12.5 mm, 134.2 kHz SST full duplex) into the pelvic girdle with a hypodermic syringe before returning them to the river.

Five stationary PIT tag interrogator sites were used to quantify movements of mountain whitefish between the Methow and Columbia rivers and areas within the Methow River basin from July 2009 to April 2013 (Fig. 1). To maximize the probability of detection of tagged fish, as well as to determine the direction of individual fish movement, each site was equipped with two arrays of three to six antennas per array. The antennas were systematically numbered in a successively downstream manner, river left to river right. When a fish with a PIT tag passed an antenna, the unique tag number, date, and time were recorded. Only one array was present at the site near the mouth of the Methow River (LMR) during 2009 and most of 2010, with a second array added on 2 December 2010.

We used rules described in Connolly et al. (2008) to identify a fish passage event and the direction of movement. Briefly, we identified downstream-directed movements as those when a fish was (1) detected at an upstream antenna and then a downstream antenna at the same interrogator site within an 18 min interval, which corresponded to the 95th percentile of the time for mountain

Fig. 1. River network in the Methow River basin and its connection to the upper Columbia River, Washington, USA. The shaded squares identify PIT tag interrogator systems, the open bar shows the weir in the Twisp River, and the shaded polygon denotes the range of locations where mountain whitefish were collected and tagged. Circles identify locations of water samples and where otoliths of mountain whitefish were extracted (closed circles) or not (open circles).



whitefish to pass an interrogator site, (2) detected at an antenna at one interrogator site (e.g., mouth of Twisp River) and then subsequently detected at a second interrogator site (e.g., LMR) within a 3-week period, which corresponded to the time for approximately 95% of the fish to make the longer distance migration, or (3) detected moving past an antenna at the same time of year when other fish were moving downstream based on rules 1 and 2. Similar rules were used to identify upstream movements.

Detection efficiency of each interrogator site was estimated using a two-array detection probability model in the USER program (Lady et al. 2003). Detections of mountain whitefish were categorized as the number of fish detected on the upper array only, the lower array only, or the number detected on both arrays. Variations around these estimates were determined by the Delta method (Seber 1982, pp. 7–9). At LMR when only one array was present during 2009 and 2010, the average detection efficiency was 45% when fully operational and 38% after accounting for the time antennas were inoperable (following Homel and Budy 2008). When

the second array was added, the average detection efficiency increased to 65% when fully operational and 45% after accounting for inoperable antennas.

Otolith chemistry and macrostructure

We collected water samples from seven locations within the Methow River basin and Columbia River for analysis of strontium (Sr) isotopes (Fig. 1). Samples were filtered (0.45 μm), acidified with HNO_3 , and frozen until analysis. Water samples were analyzed at the Interdisciplinary Center for Plasma Mass Spectrometry (University of California–Davis). Strontium isotopic ratio ($^{87}\text{Sr}:^{86}\text{Sr}$) was determined using a multicollector inductively coupled plasma mass spectrometer (MC-ICPMS) and normalized relative to the National Institute of Standards and Technology (NIST) SRM987 ($n = 9$, 0.71025 ± 0.00001 (mean \pm 2 SD)). Values for $^{87}\text{Sr}:^{86}\text{Sr}$ in the water we collected were similar to those reported by others (Barnett-Johnson et al. 2010; Miller et al. 2011) for the Methow River and upper Columbia River basins (Table 1; Table S1¹). There-

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2013-0279>.

Table 1. Locations where water samples were collected in the Methow River basin and in the Columbia River above Wells Dam, riverine $^{87}\text{Sr}:^{86}\text{Sr}$ values, and the number of mountain whitefish from which otoliths were collected and that exhibited single and multiple migrations to the Columbia River.

Location	rkm	$^{87}\text{Sr}:^{86}\text{Sr}$	Fish collected for otoliths	Migratory fish	Repeat migrations
Upper Methow River	89	0.70423	10 (4)	1	1
Methow River	76	0.70420	20 (20)	6	5
Methow River	69	0.70424	21 (21)	9	7
Methow River	15	0.70427	0	—	—
Chewuch River	99	0.70411	11 (3)	0	0
Twisp River	88	0.70442	13 (3)	2	0
Columbia River	7	0.71463	0	—	—

Note: The numbers in parentheses identify the sample size used for otolith macrostructure analyses. "rkm" is the distance from the mouth of the Methow River.

fore, we assumed seasonal and annual variation was minimal, in a manner consistent with other studies (Kennedy et al. 2000; Clarke et al. 2007; Muhlfeld et al. 2012, but see Wells et al. 2003; Crook et al. 2013).

To increase our understanding of the movement patterns that were observed with the tagged mountain whitefish, we collected and analyzed otoliths from 75 fish across five locations in the Methow River basin (Fig. 1; Table 1). We attempted and were unable to collect mountain whitefish from the Columbia River. None of the fish used in the otolith analysis had PIT tags. To minimize chemical contamination, otoliths were extracted using plastic forceps and stored in vials. Otoliths were cleaned and rinsed in ultrapure water and then polished with waterproof silicon carbide paper on both sides in the sagittal plane to just above the plane of the nucleus, while simultaneously taking care to preserve the edges. Polished otoliths were mounted on slides in randomized groups ($n = 12$; Donohoe and Zimmerman 2010), sonicated for 30 s in ultrapure water, given a final rinse, and air-dried in a Class-100 clean bench prior to analysis.

To quantify $^{87}\text{Sr}:^{86}\text{Sr}$ in the otolith, we used laser ablation MC-ICPMS (LA-MC-ICPMS; NuPlasma multicollector with a Nu-Wave DUV193 excimer laser at the College of Ocean and Atmospheric Sciences, Oregon State University) along a transect running from the core to the pararostrum at an average angle of 198.82 degrees ($SD = 8.04$) clockwise from vertical (core to pararostrum). The laser was set at a pulse rate of 10 Hz, ablation spot size of 65 μm , and a travel speed of 10 $\mu\text{m}\cdot\text{s}^{-1}$. The $^{87}\text{Sr}:^{86}\text{Sr}$ values of the otolith were corrected by the session mean $^{87}\text{Sr}:^{86}\text{Sr}$ of a marine gastropod (0.70929 ± 0.0002) run every fifth sample, relative to the global mean value (0.70918) for this material. Using linear regression, we compared the mean $^{87}\text{Sr}:^{86}\text{Sr}$ of the first 20 points along the edge of the otolith with values in the ambient water from which the fish were collected. Because we did not collect mountain whitefish from the Columbia River, we could not compare relationships between otoliths and water in this location. However, otoliths from sculpin, which we assumed to be nonmigratory, were collected from the same location as the whitefish, as well as in the Columbia River, allowing an approximated comparison. We did not find a difference in $^{87}\text{Sr}:^{86}\text{Sr}$ at the otolith edge and ambient water in the Methow River between mountain whitefish and sculpin ($P = 0.35$). Thus, we combined the two fish species so values from the Columbia River could be included in the comparison between $^{87}\text{Sr}:^{86}\text{Sr}$ in water and otoliths. We found a linear relationship between $^{87}\text{Sr}:^{86}\text{Sr}$ at the edge of the otolith and that in ambient water ($^{87}\text{Sr}:^{86}\text{Sr}_{\text{otolith}} = 0.0198 + 0.9718(^{87}\text{Sr}:^{86}\text{Sr}_{\text{water}})$, $r^2 = 0.96$, $n = 89$). The slope was not significantly different from 1 ($P = 0.19$) nor was the intercept different from 0 ($P = 0.19$), confirming that no fractionation had occurred.

For a subset of whitefish ($n = 51$), the isotopic data collected from the otoliths were linked to their macrostructural features to estimate the age at first migration and each subsequent migration, as well as to estimate the approximate growth of migrants compared to nonmigrants (Table 1). Alternating bands of light and dark zones in the otolith were assumed to indicate rapid summer growth and slower winter growth (annulus), respectively, which when combined represent 1 year of growth (Radtke et al. 1998). Distances from the core of the otolith to the onset and termination points of each annulus were measured along the isotopic laser ablation transect from the core to the pararostrum in Image Pro Plus (Media Cybernetics, Bethesda, Maryland). In addition, we used counts of annuli on each otolith and a subset of scales ($n = 44$; Bellmore et al. 2013) to age each fish.

There was a linear relationship between otolith radius (OR; measured along the isotopic transect from core to pararostrum) and fork length (FL) at time of capture ($FL = 44.76 + 0.121(\text{OR})$, $r^2 = 0.86$, $n = 51$). The linear regression relationship was then adjusted by a correction factor, which was the ratio of the observed body length to the estimated body length (Francis 1990). This relationship was used to reconstruct individual length-at-age estimates at the onset and termination points of the annuli, which were used to calculate growth. Growth was estimated as the change in back-calculated length between annuli. Although this regression method tends to underestimate back-calculated length-at-age, and in turn growth (Campana 1990), we assumed it would be a conservative measure of the relative differences between migrants and nonmigrants.

Data analyses

General patterns of movement exhibited by mountain whitefish were assessed by summarizing annual upstream and downstream movements from passive detection of fish at each PIT tag interrogator site and from $^{87}\text{Sr}:^{86}\text{Sr}$ and macrostructure profiles from the otolith. For each methodology, we estimated the proportion of mountain whitefish that migrated to the Columbia River by dividing the number of individuals that moved by the total number of individuals. For PIT-tagged fish, we corrected this proportion with the detection efficiency at LMR (Al-Chokhachy and Budy 2008). The proportion of individuals exhibiting repeat migrations in subsequent years was estimated similarly, but only those identified as migrants were used in the calculations.

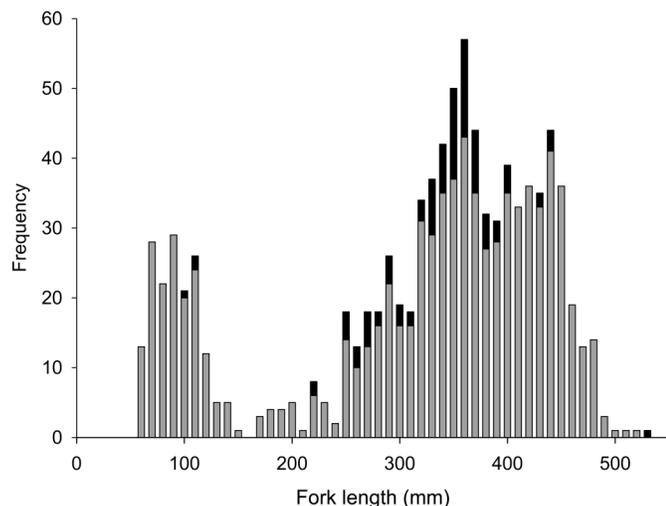
Size and growth comparison between migrants and nonmigrants

Because of the movement to a potentially more productive habitat (i.e., Columbia River), we predicted length and growth of similarly aged individuals to be greater for migrants than nonmigrants (Chapman et al. 2011). We tested this prediction using a one-way analysis of variance (ANOVA) to compare differences in length-at-age and growth between migrant and nonmigrant mountain whitefish that moved to the Columbia River. For tagged fish, mean length at time of tagging was compared between migrants and nonmigrants. For otolith data, we compared mean back-calculated length and growth at the beginning and terminal points of each annuli between migrants and nonmigrants. All models met assumptions of normality and equal variances.

Biotic and abiotic factors influencing migration

We evaluated two aspects of mountain whitefish migration between the Methow and Columbia rivers. First, we predicted that larger individuals and those closer to the Columbia River to be more likely to migrate, which is consistent with studies of other nonanadromous salmonids (Olsson et al. 2006; Al-Chokhachy and Budy 2008; Young 2011). We used logistic regression to determine the importance of fish length and distance from the mouth of the Methow River (km) at time of tagging in predicting the probability of movement. Logistic regressions were first done for all fish tagged and then for only the migrant fish to evaluate repeat move-

Fig. 2. Length–frequency distribution of mountain whitefish in the Methow River at time of PIT tagging for fish that moved to the Columbia River (black bars) and fish that remained in the Methow River and its tributaries (gray bars).



ments. Preliminary visual assessment of scatter plots suggested a nonlinear relationship between fork length and movement behavior when all fish were considered. Hence, for this model, we included a quadratic variable for length. Overdispersion (Pearson χ^2 divided by degrees of freedom, df) and lack-of-fit (Hosmer–Lemeshow goodness-of-fit test) were checked for each logistic model (Allison 1999).

Second, we used linear regression to assess the influence that temperature and discharge, measured near the mouth of the Methow River, had on the proportion of migrants and the timing of migration. We chose water temperature and discharge because these can directly influence behavior of fish (Gowan and Fausch 1996; Homel and Budy 2008; Young 2011), as well as other environmental factors such as nutrient and food availability (Brodersen et al. 2011). Although water temperatures were measured for most of the duration of the study, it was not measured continuously. To fill in the gaps, we used a nonlinear air–water temperature relationship (Mohseni et al. 1998), which has been used successfully in this region (Benjamin et al. 2013). Air temperature recorded at a weather station near the mouth of the Methow River was obtained from the National Climate Data Center (<http://www.ncdc.noaa.gov/oa/ncdc.html>). For both proportion of migrants and timing of migration, we used mean daily water temperature and discharge for the season prior to the migratory event, which was determined from PIT tag data. For example, if fish migrated to the Columbia River in the autumn, then mean summer temperature was used in the analysis. We chose the prior season because we assumed this would encompass the growing conditions (i.e., peak food availability) prior to migration (Brodersen et al. 2011). Each migratory year was considered a sample ($n = 4$). For the analysis of the proportion of migrants, we were able to include three additional years (2005, 2007, and 2008) from the otolith data that were not covered with the PIT tag data. However, this was not possible for the analyses of migration timing because we could not pinpoint the exact timing of migration owing to methodological limitations. We conducted the analyses for temperature and discharge separately to account for the small sample size.

Results

Movement patterns

We observed 99 of the 915 tagged mountain whitefish exhibit seasonal movements from the Methow River to overwintering habitats in the Columbia River. Mean (\pm SE) FL and mass of tagged

Fig. 3. Number of mountain whitefish that migrated and timing of migration between the Methow (positive values) and Columbia (negative values) rivers for migrations that began in 2009 (black bars), 2010 (open bars), 2011 (stippled bars), and 2012 (gray bars). Migrations began in approximately September of one year and ended in the spring of the following year. For example, fish that migrated into the Columbia River in 2009 returned to the Methow River in spring 2010.

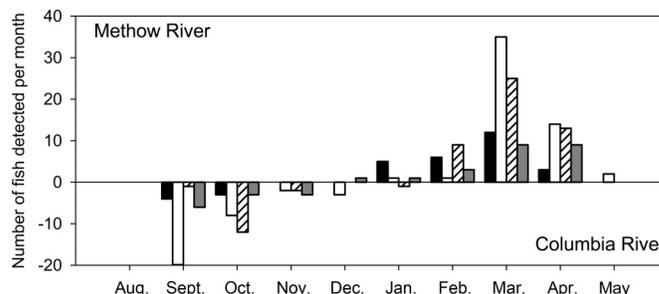


Table 2. Estimated mean length-at-age (\pm 95% CI) for fish that moved to the Columbia River (migrants) and fish that remained in the Methow River (nonmigrants), propensity to migrate by methodology, and the median (range in parentheses) number of years between tagging and migration.

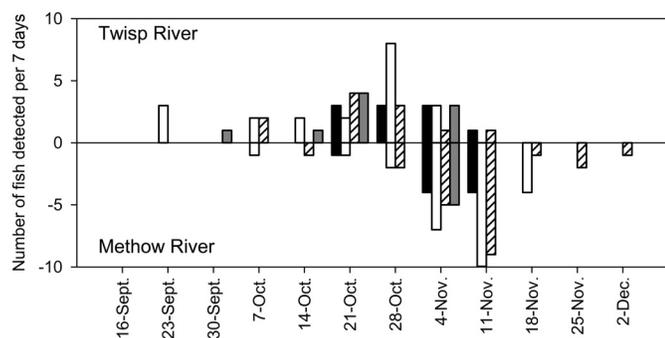
Age	Length (mm)		Propensity to migrate (%)		Post-tagging interval (year)
	Nonmigrants	Migrants	PIT tag	Otolith	
1	87.8 (3.3)	104.0 (12.4)	—	29	1
2	198.3 (8.0)	212.5 (6.4)	17	17	0
3	254.8 (3.1)	257.5 (5.3)	16	0	0 (0–2)
4	288.4 (2.5)	287.7 (7.5)	18	8	0 (0–2)
5	328.4 (1.9)	328.5 (4.8)	15	14	0 (0–3)
6	358.9 (1.5)	356.7 (2.5)	28	0	0 (0–3)
7	381.8 (1.8)	379.6 (6.3)	67	0	0 (0–1)
8	400.1 (1.4)	394.8 (4.0)	39	0	0
9	420.7 (1.6)	427.0 (25.4)	18	0	0
10	438.2 (1.1)	434.3 (2.9)	13	0	0
11+	464.1 (3.9)		4	0	0

Note: Ages were based on otolith and scale analysis. Propensity to migrate is based on all fish sampled per methodology and includes repeated migrations made by individual fish.

fish were 313 ± 3.9 mm (range: 56–522 mm) and 502.8 ± 14.0 g (1.3–1752 g), respectively (Fig. 2). After accounting for the detection efficiency of the antennas, the estimated percentage of tagged fish exhibiting migratory behavior to the Columbia River was 25%. Downstream-directed movements to the Columbia River occurred in autumn (September–October), and return migrations occurred the following spring (February–April; Fig. 3). The majority of fish migrated the same year as being tagged, except those that were age-1, which migrated the following year (Table 2). Although most of the mountain whitefish that moved to the Columbia River were not detected again until returning to the Methow River the following spring, we did detect four fish that moved past dams and (or) into another tributary (i.e., Entiat River). For example, one fish (tag ID: 3D9.1C2CEAF788) tagged in August 2010 moved past three dams (i.e., Wells, Rocky Reach, and Rock Island dams) in the Columbia River and traveled up to 185 km (one-way) before returning to the Methow River in March 2013.

Seasonal spawning migrations were also apparent for mountain whitefish moving between the mainstem Methow River and its tributaries (see Fig. 4 for an example). We observed 69 of the 915 tagged fish making these migrations, with 49% consistently

Fig. 4. Weekly number of mountain whitefish that migrated between the Twisp (positive values) and Methow (negative values) rivers in 2009 (black bars), 2010 (open bars), 2011 (stippled bars), and 2012 (gray bars). Similar timing of migration occurred for the Chewuch and upper Methow rivers.



returning to the same tributary year after year. On average, individual fish spent 12 days (± 2.6 days SE) within the tributaries before returning to the mainstem Methow River. Six of the fish that moved into tributaries would then migrate to the Columbia River to overwinter.

Across the otolith transect, we observed expected patterns of $^{87}\text{Sr}:^{86}\text{Sr}$ for the Methow River of 0.704 (± 0.0003 SD) and the Columbia River of 0.715 (± 0.001 SD; Fig. 5). Of the 75 mountain whitefish used for otolith analysis, 57 fish (76%) had $^{87}\text{Sr}:^{86}\text{Sr}$ isotopic ratios of 0.704 consistently across the otolith transect, whereas 18 fish (24%) exhibited variable isotopic ratios that fluctuated between 0.704 and 0.716. Of the fish with variable isotopic profiles, 10 fish exhibited peak isotopic ratios of 0.713 and 0.716, consistent with Columbia River values. Profiles of eight individuals had peak $^{87}\text{Sr}:^{86}\text{Sr}$ between 0.708 and 0.712 (0.709 ± 0.001), which may indicate movements and residence time in environments that were a mixture of the Methow and Columbia rivers (i.e., confluence). Most of the migrants (15 out of 18) were captured in the mainstem Methow River as opposed to the tributaries (Chewuch, Twisp, and upper Methow rivers; Table 1).

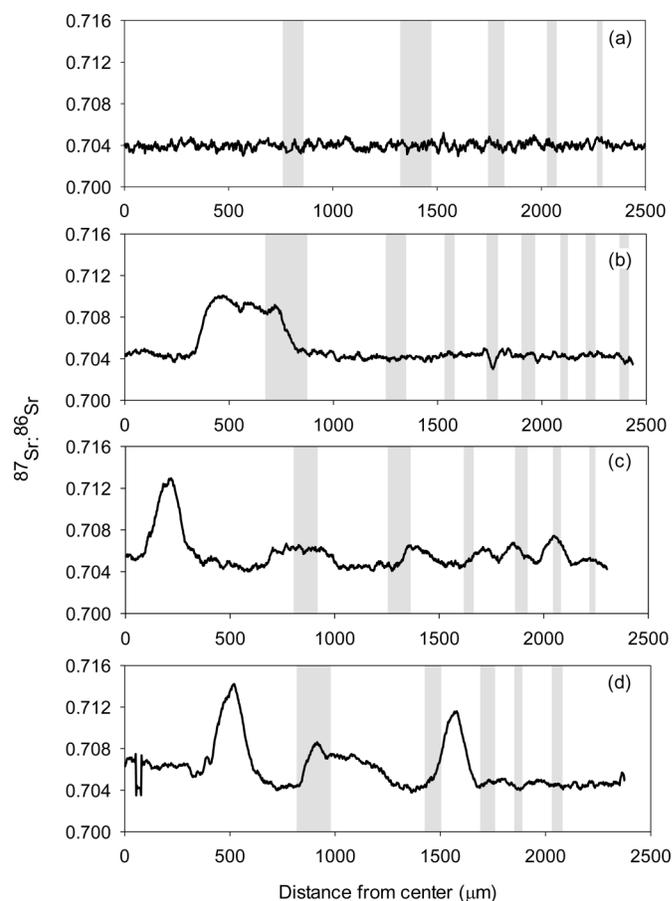
Combining isotope profiles of the otolith with its macrostructure allowed us to approximate age of movement and seasonal timing. Otolith $^{87}\text{Sr}:^{86}\text{Sr}$ profiles integrated with macrostructure data showed that the majority of individuals that migrated to the Columbia River did so initially as juveniles at age-0 (83%) and to a lesser extent at age-1 (17%). Peaks in $^{87}\text{Sr}:^{86}\text{Sr}$ typically overlapped with one or more annuli along the otolith transect, which would correspond to periods of slower growth likely associated with cooler temperatures (i.e., autumn and winter; Fig. 5).

Both methodologies showed similar proportions of individuals making repeat migrations between the Methow and Columbia rivers. From PIT tagging data, we estimated 58% ($n = 57$) exhibited repeat migrations in consecutive years, and otolith data estimated 72% ($n = 13$) to exhibit repeat migrations (Table 1). Combining otolith macrostructure and $^{87}\text{Sr}:^{86}\text{Sr}$ suggested that these fish would continue to move between the Methow River and Columbia River up to age-5 (Fig. 5; Table 2). In contrast, PIT-tagged fish were observed to migrate up to age-11.

Size and growth comparisons between migrants and nonmigrants

Mean length-at-age at the time of tagging was consistently larger for mountain whitefish that moved to the Columbia River at ages-1 and -2 when compared with similarly aged fish that remained in the Methow River ($P < 0.001$; Table 2). Beyond age-2, no difference was observed ($P > 0.08$). In contrast, back-calculated mean length-at-age was not different between similarly aged migrants and nonmigrants based on otolith analysis ($P > 0.09$). Estimated growth from back-calculated length was also similar across

Fig. 5. Examples of combined $^{87}\text{Sr}:^{86}\text{Sr}$ and macrostructure profiles along the otolith transects from four individual whitefish. The otolith transect was divided into alternating bands, which represent the annuli produced when growth is slower (grey bands) or periods when growth is greater (white bands). Profiles show (a) a 5-year-old mountain whitefish (300 mm) captured in the lower Methow River that did not migrate to the Columbia River, (b) an 8-year-old fish (390 mm) captured in the Twisp River that exhibited one migratory event, (c) a 6-year-old fish (340 mm) captured in the lower Methow River that exhibited at least one and possibly multiple migratory events, and (d) a 5-year-old fish (368 mm) captured in the lower Methow River that exhibited multiple migrations.



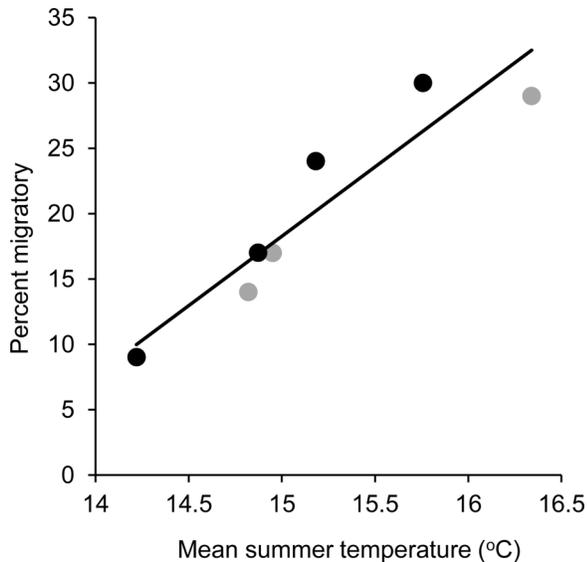
all age classes between fish that migrated to the Columbia River and those that did not ($P > 0.16$).

Biotic and abiotic factors influencing migration

The probability of migration to the Columbia River was related to the length of the fish at time of tagging. However, it was the intermediate sized fish (200–400 mm) that had a higher probability to have migrated compared with smaller and larger fish (length: $P < 0.001$; length²: $P < 0.001$). In contrast with our predictions, distance from the mouth of the Methow River at time of capture did not have an effect on movement to the Columbia River ($P < 0.91$). The probability of making repeat migrations increased by 1% for each millimetre increase in FL at time of tagging ($P = 0.04$, estimated odds ratio = 1.01 (1.0–1.02 95% CI)), but distance from the mouth of the Methow River was not influential ($P = 0.72$). We did not observe a relationship between seasonal spawning movements to tributaries and fish length or distance from the confluence of the respective tributary at time of capture.

The proportion of mountain whitefish departing from the Methow River in the autumn increased with warmer mean sum-

Fig. 6. The percentage of the tagged mountain whitefish (black circles) and those collected for otoliths (gray circles) that exhibit seasonal migrations (approximately September–April) from the Methow River basin to the Columbia River, Washington, USA, in relation to mean summer temperature (July–September).



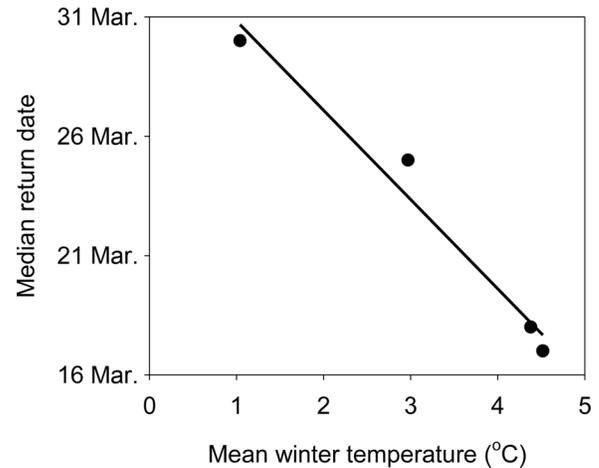
mer temperature ($P < 0.01$, $R^2 = 0.87$, $n = 7$), but not with mean discharge during the summer ($P = 0.98$, $n = 7$; Fig. 6). The median departure and return dates occurred earlier when the previous season's temperatures were warmer, but this was only significant for mountain whitefish returning to the Methow River from the Columbia River ($P = 0.01$, $R^2 = 0.97$, $n = 4$; Fig. 7). In contrast, timing of migration occurred later with increasing discharge, but this was not significant ($P > 0.15$).

Discussion

Previous studies have observed mountain whitefish making seasonal migrations to both overwintering and spawning habitats (Pettit and Wallace 1975; Davies and Thompson 1976; Baxter 2002). However, knowledge of the extent of the population exhibiting migrations was largely unknown, as well as potential causes and consequences of migration. Moreover, most studies on mountain whitefish have been unable to quantify or even observe juveniles. We provide a comprehensive study on the migratory behavior of mountain whitefish in a river network, and it confirms many of the patterns observed or speculated by others (Pettit and Wallace 1975; Davies and Thompson 1976; Baxter 2002; Lance and Baxter 2011). In addition, we fill knowledge gaps regarding the presence of juveniles in those previous studies by revealing that some juveniles use large river habitats for early rearing. We demonstrated that approximately 25% of the sampled mountain whitefish moved from the Methow River downstream up to 185 rkm to overwinter in the Columbia River and that movement was related to body size and water temperature. By coupling PIT tag technology over four migratory years with otolith Sr isotopes, we were able to assess movement behavior across multiple age classes of mountain whitefish over multiple spatial scales.

Our study quantifies the migration of mountain whitefish during their first year of life and is consistent with patterns observed for juvenile mountain whitefish in other regions (Davies and Thompson 1976), as well as humpback whitefish (*Coregonus pidschian*; Neilson 2010) and other nonanadromous salmonids (e.g., Al-Chokhachy and Budy 2008; Muhlfeld et al. 2012). We detected only 5 of the 152 age-1 or younger PIT-tagged mountain whitefish migrating to the Columbia River, and all those individuals migrated 1 year after tagging. In contrast, Sr isotopes in otoliths

Fig. 7. The median return date to the Methow River in relation to the mean winter (January–March) water temperature ($P = 0.01$, $R^2 = 0.97$) during four consecutive migration years.



revealed that first migration to Columbia River was primarily at age-0 and secondarily at age-1. This early age at first migration exhibited by mountain whitefish may explain why we found it difficult to quantify migration of these age classes via PIT tagging (i.e., individuals migrated prior to sampling or were too small to receive a PIT tag), as well as why other investigators found it difficult to observe and quantify these age classes (Baxter 2002; Meyer et al. 2009; Lance and Baxter 2011). Our results suggest that a portion of the mountain whitefish population require connectivity to large river habitats to complete their life cycle. Whether fewer or more juveniles migrate to a large river that is regulated, like the Columbia River, and what the potential consequences are of disconnecting the existing river networks remain unknown.

Variation in movement behavior among individuals within a population, such as we observed in this study, is common among fish species (Jonsson and Jonsson 1993; Chapman et al. 2012). Two contrasting hypotheses regarding body size exist to explain these differing behaviors. Within an age group, smaller individuals may be more likely to migrate because of physiological intolerances during certain seasons, whereas larger individuals may be more likely to migrate owing to inadequate food resources to meet their metabolic demand (Olsson et al. 2006; Benjamin et al. 2013). We observed a greater length at tagging of age-1 and age-2 migrants compared with similarly aged nonmigrants, which supports the second hypothesis. This observation may also suggest a critical size threshold must be reached before migration (Bohlin et al. 1996). However, most tagged individuals exceeded a critical size without migrating, and back-calculated length from otoliths was similar between migrants and nonmigrants. Thus, it is likely that size interacts with growth, lipid content, and other physiological factors, as well as environmental conditions, to determine a migratory tactic, as has been observed for other salmonids (Morinville and Rasmussen 2003; Thériault and Dodson 2003; McMillan et al. 2011).

In addition, the adoption of one life history form over the other is hypothesized to be a trade-off between costs and benefits of migration (Chapman et al. 2011). If so, migratory fish should exhibit faster growth and greater fitness than nonmigrants (Thériault and Dodson 2003). We did not find evidence that growth rates differed between mountain whitefish that overwintered in the Columbia River compared with those that remained in the Methow River. Jonsson and Jonsson (1993) suggested that migratory individuals may have a greater metabolic rate, and movement to a more productive habitat (i.e., the Columbia River) would be necessary to maintain a similar size and growth trajectory as nonmi-

grants. If so, this may explain the similarity in back-calculated estimates of length and growth between migrants and nonmigrants. Moreover, females often dominate the migratory contingent in other species (Jonsson and Jonsson 1993; Chapman et al. 2011) and may allocate a higher proportion of consumed energy to reproductive costs relative to the proportion to growth. This pattern may be the same for mountain whitefish, but was not part of this study.

We observed that individuals tagged at intermediate sizes (200–400 mm) were more likely to migrate to the Columbia River. This pattern is inconsistent with previous observations of large (350–550 mm) mountain whitefish migrating long distances (Baxter 2002) and research by others (Monnot et al. 2008; Young 2011) that have observed larger salmonids were more likely to migrate. In our study, the low propensity for larger tagged fish to migrate was consistent with fish collected for otolith analysis, where migrations were no longer apparent after age-5. Perhaps older migrants were not observed from otolith data because the average width of winter growth on the otolith after age-4 (25–62 μm range) was smaller than the laser spot diameter (65 μm), homogenizing the signal (Outridge et al. 2002). This may explain why higher Sr isotope peak values tended to occur close to the core, while intermediate values were observed further along the transect. A higher precision analysis resulting in a smaller spot size (i.e., ion microprobe analysis; Radtke et al. 1998; Sano et al. 2008) may be more suitable for identifying seasonal movements; however, there are trade-offs in cost and availability. Given the high propensity of juvenile mountain whitefish to migrate revealed from otoliths and the low propensity of large adults to migrate observed from both methodologies, migration may actually be negatively related to body size, as described for arctic grayling (*Thymallus arcticus*; Hughes 2000).

The proportion of migratory mountain whitefish and timing of their migration was explained by water temperature, but not river discharge, which is similar to that observed for bull trout (Hornell and Budy 2008; Monnot et al. 2008). We observed that warmer summer temperatures led to a greater proportion of mountain whitefish migrating to the Columbia River. This relationship may be related to the ability of individuals to accumulate sufficient energy stores before making seasonal migration (Brodersen et al. 2011) or to a size threshold that needs to be reached that would reduce predation risk (Brönmark et al. 2008). Similarly, warmer temperatures led to earlier return dates to the Methow River, which may be owing to perceived timing of food resources in the destined habitat (Schindler et al. 2005; Brodersen et al. 2011). Yet caution must be taken in interpreting how temperature may affect mountain whitefish migration because of the low sample size. Regardless, our results suggest that mountain whitefish may adjust the timing of migration to changes in environmental conditions, and our investigation of the relationship with temperature and discharge are a first step. Moreover, because temperature and discharge are likely to be altered owing to climate change, the migratory tactic exhibited by mountain whitefish may change, as model simulations identified for *O. mykiss* in the Methow River basin (Benjamin et al. 2013).

Spawning migrations are common among fish species (Jonsson and Jonsson 1993), including mountain whitefish (Northcote and Ennis 1994). In the Methow River basin, we observed rapid movements of PIT-tagged mountain whitefish into larger tributaries during late October. These fish returned to the main stem in early November, which we assumed was primarily a spawning migration. In addition, approximately 50% of these individuals consistently made seasonal migrations into the same tributary over consecutive years. Based on these results, we believe this to be evidence for a strong homing behavior, which corroborates observations by others (Davies and Thompson 1976).

By coupling otolith analysis and PIT tag technology, we were able to identify variation in movement behavior among mountain

whitefish in a large river network. Otolith data revealed lifetime movement behavior over broad spatial and temporal scales, as well as age and size at movement. However, otolith data cannot reveal detailed movements such as daily and seasonal timing to overwintering and spawning habitats, which was provided by PIT tagging. Moreover, movement detected via PIT tagging can be linked to individual traits and environmental factors. Yet, PIT tagging is limited because of the constraints of tagging juvenile fish <60 mm, as well as the inability of detecting fish in portions of the river network without antennas. If only one methodology was used, we would have been restricted in our understanding and inference. For instance, if we only used otoliths, we would have identified patterns in migration of mountain whitefish from the Methow River to the Columbia River, age at migration, and comparisons of growth between migrants and nonmigrants, but we would not have been able to pinpoint exact timing of migration, movement within the Methow River basin, or potential causes of movement (i.e., fish length, temperature, and discharge). Thus, it appears that the complementary use of these two methods provides an efficient means to understanding patterns of movement of fish species and the potential population-level consequences of this behavior.

In addition, combining otolith with telemetry data may be particularly useful when migratory and nonmigratory fish cannot be identified by size, as is the case with most nonanadromous fish (Jonsson and Jonsson 1993). Surprisingly, only three other studies have combined otolith analysis with telemetry, such as passive telemetry (i.e., PIT tagging; Downs et al. 2006), radiotelemetry (Brenkman et al. 2007), or acoustic telemetry (Honda et al. 2012), to obtain a more complete understanding of migratory salmonids. Perhaps the lack of studies using both methods is because a fish must be sacrificed to obtain the otoliths, which could be undesirable for endangered or threatened species. However, opportunistic use of accidental mortalities and carcasses found while sampling could offer opportunities to extract otoliths that could be stored for future use (e.g., Downs et al. 2006; Miller et al. 2011). Alternatively, the use of nonlethal methods (e.g., scales and fin rays) for age and life history reconstructions may be used to maximize the information obtained from each fish and minimize impacts on endangered populations (Wells et al. 2003).

The movements of fish operate on varying spatio-temporal scales (Schlosser and Angermeier 1995), which can be difficult to monitor (Fausch et al. 2002; Fullerton et al. 2010). The methodologies we used provide a more comprehensive approach to understanding spatial connectivity and animal behavior. However, more research is needed to assess the potential causes of movement at different scales. One approach would be to use experimental manipulations, such as translocations of a fish species or community to investigate density dependence and competition-predation effects, or food manipulations to further assess motivation of movement. Moreover, the consequences of movement on trophic dynamics, community structure, and ecosystem services are still unclear. For example, mountain whitefish that overwinter in the Columbia River may transport and excrete phosphorus and nitrogen to the Methow River (Lance and Baxter 2011), which could lead to bottom-up stimulation of resources available to the fish community. Finally, river networks encompass a fish community, which is largely composed of understudied fish that display varying movement patterns (Baxter 2002; Albanese et al. 2004; Petty and Grossman 2004). Therefore, it is important to understand the biology and ecology of the entire community. Until this happens, successful conservation of fish populations and communities, river networks, and ecosystems will be limited.

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