Body morphology differs in wild juvenile Chinook salmon *Oncorhynchus tshawytscha* that express different migratory phenotypes in the Willamette River, Oregon, U.S.A.

E. J. Billman*†, L. D. Whitman‡, R. K. Schroeder‡, C. S. Sharpe‡, D. L. G. Noakes*§ and C. B. Schreck*‖

Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall Corvallis, OR 97331, U.S.A., ‡U.S. Geological Survey, Oregon Department of Fish and Wildlife, 28655 Highway 34, Corvallis, OR 97333, U.S.A., §Oregon Hatchery Research Center, 2418 East Fall Creek Road, Alsea, OR 97324, U.S.A. and ‖U.S. Geological Survey, Oregon Cooperative Fish and Wildlife Research Unit, Oregon State University, 104 Nash Hall, Corvallis, OR 97331, U.S.A.

Body morphology of juvenile Chinook salmon *Oncorhynchus tshawytscha* in the upper Willamette River, Oregon, U.S.A., was analysed to determine if variation in body shape is correlated with migratory life-history tactics followed by juveniles. Body shape was compared between migrating juveniles that expressed different life-history tactics, *i.e.* autumn migrants and yearling smolts, and among parr sampled at three sites along a longitudinal river gradient. In the upper Willamette River, the expression of life-history tactics is associated with where juveniles rear in the basin with fish rearing in downstream locations generally completing ocean ward migrations earlier in life than fish rearing in upstream locations. The morphological differences that were apparent between autumn migrants and yearling smolts were similar to differences between parr rearing in downstream and upstream reaches, indicating that body morphology is correlated with life-history tactics. Autumn migrants and parr from downstream sampling sites had deeper bodies, shorter heads and deeper caudal peduncles compared with yearling smolts and parr from the upstream sampling site. This study did not distinguish between genetic and environmental effects on morphology; however, the results suggest that downstream movement of juveniles soon after emergence is associated with differentiation in morphology and with the expression of life-history variation.

© 2014 The Fisheries Society of the British Isles

Key words: geometric morphometrics; life-history variation; phenotypic plasticity; Salmonidae; smoltification.

INTRODUCTION

Species of the genus *Oncorhynchus* within the family Salmonidae exhibit a diversity of life-history patterns among species as well as myriad of population-specific variants (Groot & Margolis, 1991; Quinn, 2005). In completing the anadromous life history, Chinook salmon *Oncorhynchus tshawytscha* (Walbaum 1792) display a broad array of life-history tactics including variation in age at seaward migration, length of freshwater,

estuarine and ocean residence, ocean distribution and migration patterns and age and season of spawning migration (Healey, 1991; Quinn, 2005; Moran *et al.*, 2013). Within a single population, variation in juvenile life-history tactics can be represented by as many as three to seven different rearing and migratory phenotypes (Reimers, 1971; Schluchter & Lichatowich, 1977; Carl & Healey, 1984; Schroeder *et al.*, 2007).

Juvenile life-history tactics of *O. tshawytscha* vary within and among populations and drainages as a result of genetic variation and phenotypic plasticity (Waples *et al.*, 2001; Moran *et al.*, 2013). Juvenile life-history tactics are characterized by patterns of holding, rearing and downstream movement from time of emergence in natal streams to saltwater entry of smolts. At emergence, downstream redistribution of fish may be the result of displacement due to reduced swimming ability (Thomas *et al.*, 1969; Healey, 1991). Evidence suggests, however, that downstream redistribution can also be the result of active swimming (Healey, 1991; Bradford & Taylor, 1997). Factors that influence downstream migration probably include environmental conditions (Irvine, 1986; Healey, 1991; Muir *et al.*, 1994; Beckman *et al.*, 2007; Sykes *et al.*, 2009; McCormick, 2013), intra and inter-specific interactions (Reimers, 1968; Stein *et al.*, 1972; Einum *et al.*, 2008) and physiology (Beckman & Dickhoff, 1998; Beckman *et al.*, 1998; Beckman *et al.*, 2000; Careau *et al.*, 2008; Perkins & Jager, 2011; McCormick, 2013).

Developmental and evolutionary forces cause morphological variation in juvenile salmonids, with both environment and genetics playing important roles in body shape (Carl & Healey, 1984; Currens *et al.*, 1989; Hard *et al.*, 1999; Wessel *et al.*, 2006). Body shape affects fish movement (*e.g.* burst *v.* sustained swimming and swimming endurance) in aquatic environments such that groups of fishes occupying different environments will diverge phenotypically (Webb, 1984; Langerhans *et al.*, 2003). Morphological variation in juvenile salmonids has been observed among populations (Taylor & McPhail, 1985) and among juveniles rearing in different environments (Swain & Holtby, 1989; Swain *et al.*, 1991; Tiffan & Connor, 2011). Additionally, studies have demonstrated morphological variation between juvenile *O. tshawytscha* that express different life-history tactics (Carl & Healey, 1984; Tiffan *et al.*, 2000). Lower Snake River (Washington and Idaho, U.S.A.) juvenile spring-run *O. tshawytscha* that smolt in the autumn have a distinct body shape compared with juveniles from the same population that smolt the following spring (Tiffan *et al.*, 2000).

Oncorhynchus tshawytscha in the upper Willamette River, Oregon, U.S.A. (Fig. 1), demonstrate the diversity of juvenile migratory phenotypes that can characterize *O. tshawytscha* populations. For this study, the upper Willamette River refers to the portion of the Willamette River upstream of Willamette Falls. *Oncorhynchus tshawytscha* in the upper Willamette River have a spring spawning migration because returning adults could not historically pass Willamette Falls during low flows in the late summer and early autumn. Adults spawn in the major tributaries of the upper Willamette River that drain the Cascade Mountains to the west; spawning does not occur in the Willamette River or coast range tributaries because of high summer water temperatures and the lack of spawning habitat (Dimick & Merryfield, 1945; Schroeder *et al.*, 2007). Upon emerging, juvenile *O. tshawytscha* typically follow one of the three major life-history tactics or migratory phenotypes (Zakel & Reed, 1984; Schroeder *et al.*, 2007). Two tactics can be characterized by timing of saltwater entry, which occurs soon after these fish pass downstream of Willamette Falls: a subyearling smolt with peak migration from June to July and a yearling smolt with peak migration from
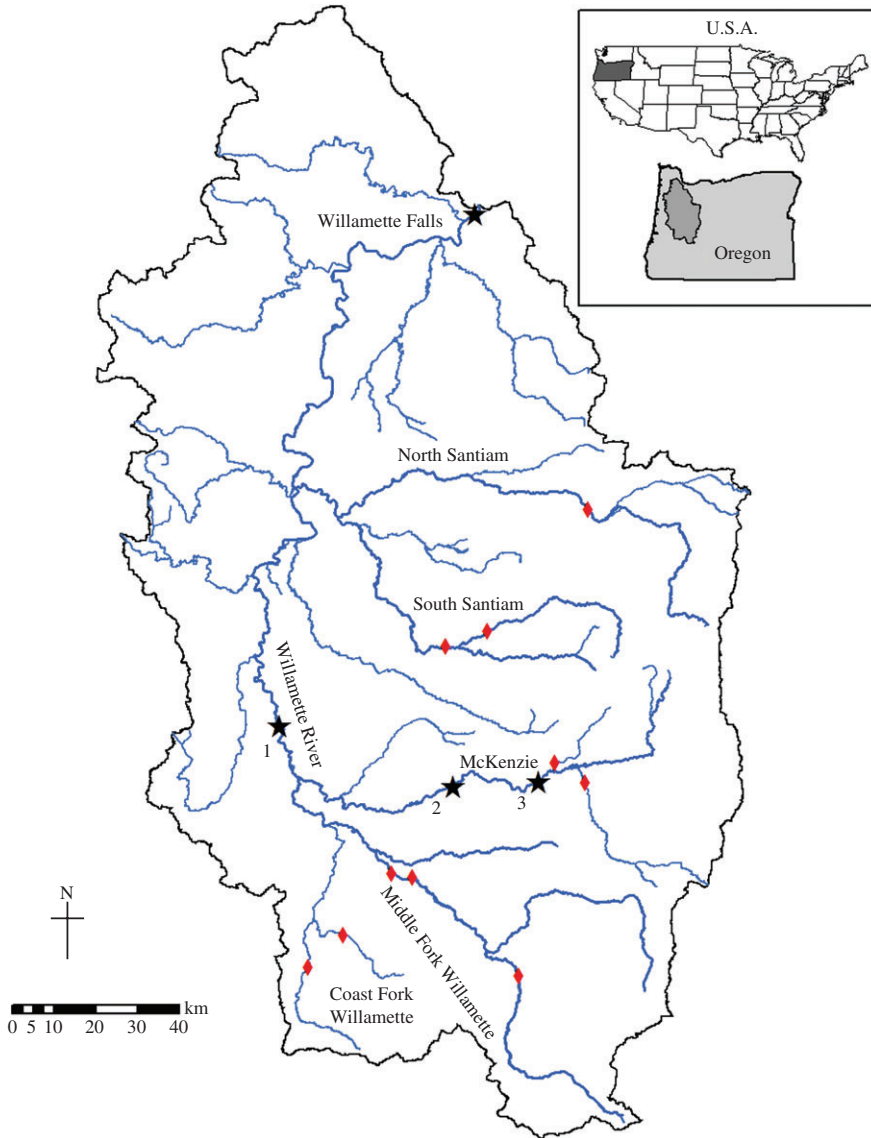
FIG. 1. Map of Willamette River Basin, Oregon, U.S.A. The upper Willamette River is considered to be the section upstream of Willamette Falls. Sampling locations are marked (★). Parr sample locations: (1) Willamette-Harrisburg: collection site on Willamette River near Harrisburg; (2) lower McKenzie: collection site on McKenzie River near McKenzie State Fish Hatchery; (3) upper McKenzie: collection site on McKenzie River at Quartz Creek Bridge (___, major rivers; ♦, flood control dams).

March to May. Juveniles that express the subyearling life-history type typically move downstream soon after emergence, rearing in the lower portions of natal tributaries and in the Willamette River. Most juveniles that express the yearling smolt life-history type typically rear in the upper reaches of natal tributaries during their first summer and overwinter in lower portions of natal tributaries and in the upper Willamette River

before smolting and migrating to the ocean in their second spring. The third major tactic is an autumn migration of juveniles (autumn migrants) with peak migration past Willamette Falls during November to December, although it remains unclear when these juveniles enter salt water. Autumn migrants comprise of juveniles that moved downstream soon after emergence, rearing in the lower portions of natal tributaries (*i.e.* downstream of river segments where spawning occurs) and in the Willamette River, and juveniles that reared in natal tributaries before migrating in the autumn. The proportion of these two groups in the autumn migrant life-history tactic varies by year and timing: early dispersers are present throughout the autumn migration while those rearing in natal tributaries are more likely to be present in late November and early December. Scale analysis would likely classify autumn migrants as yearlings, based on Gilbert–Rich notation that starts counting the age of a fish from when eggs are laid in the gravel (Schroeder *et al.*, 2007). All three life-history types may spend variable amounts of time rearing in the Columbia Estuary before migrating to the ocean.

Oncorhynchus tshawytscha in the upper Willamette River basin have been listed as a threatened species under the U.S. Endangered Species Act. Recent efforts to conserve the wild stock have focused on describing the phenotypic differences among juvenile life-history tactics, identifying their seasonal habitats and determining their relative contribution to the spawning population (Schroeder *et al*, 2007). Successful completion of these goals will guide management decisions regarding population connectivity between upper and lower portions of the basin currently fragmented by hydroelectric and flood control dams and enhancement of historic rearing habitat in lower portions of the basin. The aim of this study was to determine if variation in body morphology of juvenile *O. tshawytscha* is correlated with life-history variation as has been observed in other populations (Carl & Healey, 1984; Tiffan *et al.*, 2000). First, shape variation in the autumn migrants and yearling smolts was examined to determine if shape differed in a similar manner as observed in other *O. tshawytscha* populations (Tiffan *et al.*, 2000). Second, shape variation of parr (*i.e.* subyearling juveniles with parr marks) was examined to determine if shape differed consistently on a longitudinal river gradient such that parr from downstream locations had a body shape similar to autumn migrants and parr from upstream locations had a body shape similar to yearling smolts. The parr analysis compares fish that have previously moved downstream from spawning locations (*i.e.* downstream sites) and fish that had not yet undertaken a substantial downstream migration (*i.e.* upstream sites), thus examining the influence of downstream dispersal after emergence on body shape and life-history tactics.

MATERIALS AND METHODS

Juvenile *O. tshawytscha* were collected in the Willamette River and in the McKenzie River, one of the major spawning tributaries of the Willamette River. Only naturally produced (wild) individuals as identified by an intact adipose-fin were included in comparisons because these fish are more likely to express variable life-history characteristics than juveniles raised in hatcheries. Wild juveniles were collected during their downstream migration in the Willamette River at Willamette Falls, Oregon, U.S.A. (43 km upstream from confluence with Columbia River and 204 km from the Pacific Ocean). The fish were collected in November 2012 (autumn migrants) and from February to April 2013 (yearling smolts) from a fish trap in the juvenile fish passage facility of the Portland General Electric hydroelectric plant at Willamette Falls (Table I). Parr were collected by beach seining at one site in the Willamette River (Willamette-Harrisburg) and two sites in the McKenzie River (lower McKenzie and upper McKenzie; Fig. 1). Parr were first

TABLE I. Site, date, sample size (*n*; total number of fish from all sampling dates) and mean ± s.d. fork length (L_F), mass (*M*) and condition factor (*K*) of juvenile *Oncorhynchus tshawytscha* captured in the upper Willamette River. See Fig. 1 for location of sample sites in the upper Willamette Basin. Different lowercase letters indicate significant differences between autumn migrants and yearling smolts and among parr collection sites

Life stage	Site	Date	*n*	L_F (mm)	*M* (g)	*K*
Autumn migrant	Willamette Falls	13, 14 and 21 November 2012	8	125 ± 11[x]	21·3 ± 6·5[x]	1·06 ± 0·07[x]
Yearling smolt	Willamette Falls	11–13 February, 8–13 March and 19–23 April 2013	33	129 ± 11[x]	21·4 ± 5·6[x]	0·98 ± 0·06[y]
Parr	Willamette-Harrisburg	21 May 2013	26	81 ± 12[a]	6·2 ± 2·7[a]	1·10 ± 0·09[a]
	Lower McKenzie	3 July 2013	48	82 ± 10[a]	6·8 ± 2·4[a]	1·18 ± 0·08[b]
	Upper McKenzie	15 August 2013	44	81 ± 9[a]	5·9 ± 2·4[a]	1·07 ± 0·06[c]

collected at the downstream-most site and on progressively later dates at upstream sites so that fish were similar in size when sampled (Table I), thus avoiding confounding effects of allometry in morphometric analyses (Zelditch *et al.*, 2012). Captured fish were anaesthetized in buffered MS-222 before fork length (L_F; mm) and mass (*M*; 0·1g) were measured. Lateral images of the left side of each fish were taken with a digital camera. Fish were released upon full recovery from anaesthetic.

Fish body size was compared between autumn migrants and yearling smolts and among parr collection sites. Fulton's condition factor ($K = M L_F^{-3} \times 10^5$; Pope & Kruse, 2007) was calculated for each fish. The L_F, *M* and *K* were compared between autumn migrants and yearling smolts using a *t*-test. A one-way analysis of variance (ANOVA) was used to compare L_F, *M* and *K* among parr collection sites.

Landmark-based geometric morphometric analyses were used to compare differences in body shape between autumn migrants and yearling smolts and among parr at each sample location. A total of 15 landmarks (Fig. 2) modified from Beeman *et al.* (1994) and Tiffan & Connor (2011) were digitized to quantify body shape using tpsDig (Rohlf, 2010*a*). Shape variation from digital landmarks was summarized into relative warps (synonymous to principal components) using tpsRelw (Rohlf, 2010*b*). This procedure first removes shape variation owing to position, orientation and scale of the specimen in each image, and then uses affine and non-affine shape components from aligned specimens in a principal component analysis (PCA) to calculate relative warp scores (Rohlf & Slice, 1990). For the comparison of autumn migrants and yearling smolts, the first 14 relative warps, which combined explained >95% of the shape variation, were used as shape variables in subsequent analyses. For the parr comparison, the first 15 relative warps explained >95% of the shape variation, and were used as shape variables in subsequent analyses.

Morphometric data were analysed using mixed model multivariate analysis of variance (MANOVA) in SAS 9.2 (proc MIXED; SAS Institute; www.sas.com). Analyses for the comparison of autumn migrants and yearling smolts and for the comparison among parr were conducted separately, because in a combined analysis, shape changes due to smoltification (Beeman *et al.*, 1994) would reduce the ability to detect differences among groups within age classes. The relative warp scores were the response variables in each analysis. Relative warps are repeated measures of the same individual, so individuals were treated as a random effect. For the analysis comparing autumn migrants and yearling smolts, migrant type (levels = autumn migrant and yearling smolt) was the main effect, while for the parr
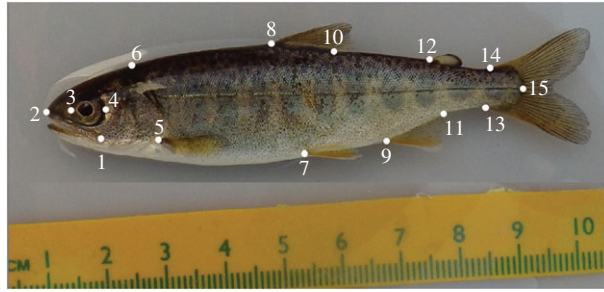
FIG. 2. Location of landmarks used for geometric morphometric analyses on juvenile *Oncorhynchus tshawytscha*. Landmarks are from Beeman *et al.* (1994) and Tiffan *et al.* (2000) with the exception of landmark 6, which is located at the posterior extent of supraoccipital along dorsal midline (beginning of nape).

analysis, collection site was the main effect. For each analysis, centroid size (*i.e.* the square root of summed squared distances from each landmark to the centre of each configuration) was a covariate in the mixed model. Because relative warps are ordered variables, an index variable that accounts for the order of relative warps must be included as a fixed categorical effect in the model along with its interactions with other fixed effects (Scott & Johnson, 2010; Wesner *et al.*, 2011; Hassell *et al.*, 2012). If the interactions with the index variable are not considered, the model will test the hypothesis that differences exist among levels of main effects when averaged across all relative warps. Relative warps are orthogonal axes of shape variation that account for decreasing amounts of total variation; as a consequence, the magnitude and direction of differences between levels of main effects on one relative warp have no bearing on differences between levels on other relative warps. The interaction between the index variable and the main effect tests for differences in shape on each relative warp independently; therefore, the interaction can be significant even if the main effect alone is not.

To determine the influence of downstream dispersal after emergence on body shape, a discriminant function analysis (proc DISCRIM; SAS Institute) was conducted to classify parr by collection site to provide a metric, *i.e.* per cent of fish correctly classified into collection site, and to determine the magnitude of shape differences. The first three relative warps were used as the dependent variables and collection site as the independent variable. Prior probability of group membership was set to be proportional to group sample size. A linear discriminant function was fitted to the data based on the results of Bartlett's modification of the likelihood ratio test (SAS Institute). A cross-validation classification technique was used to avoid a classification bias. One individual was removed from the data set, and then classified based on a discriminant function of the remaining data. This procedure was repeated for each individual in the data set. Classification rates were tested against those expected by chance using Cohen's κ (Titus *et al.*, 1984). The value of κ indicates the improvement of classification over random chance, and ranges between 0 (no improvement) and 1 (perfect assignment). The discriminant function analysis was repeated with only two groups to determine if classifications improved by combining the two downstream sites, *i.e.* those sites that included fish that had dispersed downstream after emergence.

To visualize differences in shape among groups in each comparison, thin-plate spline transformations were generated in tpsRegr (Rohlf, 2003) using superimposed landmark co-ordinates and canonical scores (Langerhans *et al.*, 2004; Hassell *et al.*, 2012). For each comparison, a canonical axis was derived from the main effect of the MANOVA (*i.e.* migrant type and collection site); however, only two levels were used in the main effect for parr with the lower two collection sites combined. Correlations between superimposed landmark co-ordinates and the main effect were generated using proc CANCOR (SAS Institute). Thin-plate spline transformations were then generated in tpsRegr using canonical scores as the independent variable and superimposed landmark coordinates as the response variable.

TABLE II. Results of mixed repeated measures multivariate analysis of variance (MANOVA) examining shape variation in juvenile *Oncorhynchus tshawytscha* in the upper Willamette River. Shape variation of individual life stages was examined to determine differences in morphology of fish exhibiting different life-history tactics

Effect	d.f.	F	P
Migrants			
Migrant type	1/343	0·09	>0·05
Centroid size	1/320	0·00	>0·05
Index variable	13/198	0·92	>0·05
Migrant type × index variable	13/198	2·48	<0·01
Parr			
Collection site	2/1069	11·46	<0·001
Centroid size	1/1128	0·02	>0·05
Index variable	14/642	0·50	>0·05
Collection site × index variable	28/897	9·67	<0·001

RESULTS

Autumn migrants and yearling smolts did not differ in L_F (*t*-test; $t_{34} = 0·84$; $P > 0·05$) or M (*t*-test; $t_{34} = 0·02$; $P > 0·05$; Table I). Autumn migrants, however, had a significantly greater K than yearling smolts (*t*-test; $t_{34} = 3·33$; $P < 0·05$). Similarly, parr did not differ in L_F (one-way ANOVA; $F_{2,139} = 0·40$; $P > 0·05$) or M (one-way ANOVA; $F_{2,139} = 2·16$; $P > 0·05$) among collection sites, but did differ significantly in K (one-way ANOVA; $F_{2,139} = 34·16$; $P < 0·001$). Fish at the lower McKenzie site had the highest K, fish at the upper McKenzie site had the lowest K and fish at the Willamette-Harrisburg site had an intermediate K (Table I).

Body morphology of autumn migrants and yearling smolts varied significantly by the interaction of migrant type and index variable [Table II and Fig. 3(a)]. Yearling smolts had more shallow and elongated bodies including a longer head and shallower caudal peduncle compared to autumn migrants (Fig. 4). Parr shape varied significantly by collection site and by the interaction of collection site by index variable (Table II). Shape was more similar between fish collected at the Willamette-Harrisburg and lower McKenzie sites compared to the upper McKenzie site [Fig. 3(b)]. Parr shape at the upper McKenzie site was more fusiform, *i.e.* shallow, elongated body with the deepest portion of the body shifted anteriorly and a shallower caudal peduncle, compared to the two downstream sites (Fig. 4).

Discriminant analysis of the parr revealed that fish from the upper McKenzie and lower McKenzie sites could be separated by collection site (Table III). Fewer parr from the Willamette-Harrisburg site, however, were classified correctly (54%); 42% of the Willamette-Harrisburg juveniles were incorrectly classified in the lower McKenzie site. The κ value indicated that correct classifications were 63% better than those expected by chance ($\kappa = 0·63$; 95% C.I. $= 0·51-0·75$; $P < 0·001$). When the Willamette-Harrisburg and lower McKenzie sites were combined, the discriminant analysis resulted in an improvement in classification as indicated by the high percentage of correct classifications (>85%; Table III) and by an increase in κ value ($\kappa = 0·82$; 95% C.I. $= 0·71-0·93$; $P < 0·001$).
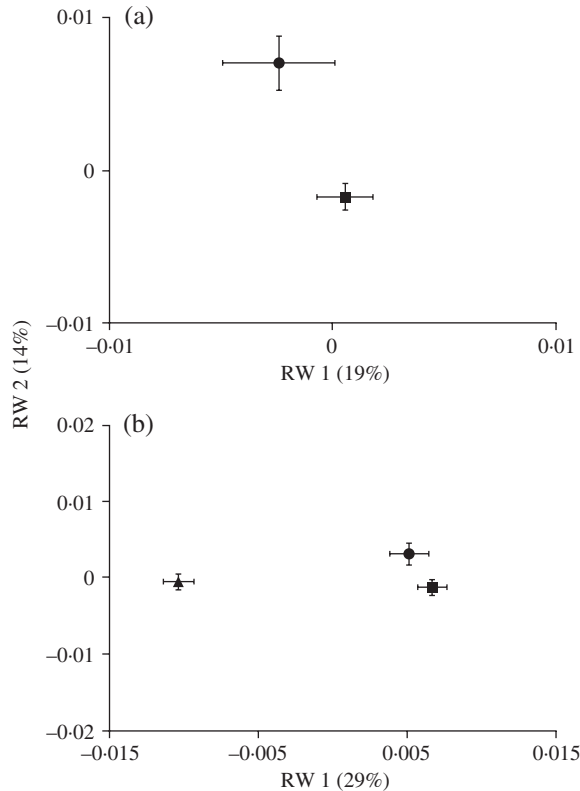
FIG. 3. Least square mean ± S.E. of relative warp (RW) scores of *Oncorhynchus tshawytscha* (a) migrants and (b) parr in the Willamette River, Oregon, U.S.A. Axes are scaled according to the relative amount of variation explained as indicated in parentheses. Migrants (a) represented by the following: autumn migrants = ●; yearling smolts = ■. Parr (b) collection sites represented by the following: Willamette-Harrisburg = ●; lower McKenzie = ■; upper McKenzie = ▲.

DISCUSSION

The differences in morphology were similar between autumn migrants and yearling smolts, and between parr rearing in downstream and upstream reaches indicating that body morphology is correlated with life-history variation in *O. tshawytscha*. Autumn migrants had deeper bodies, shorter heads and deeper caudal peduncles compared with yearling smolts in a similar manner as has been observed in other populations of *O. tshawytscha* (Tiffan *et al.*, 2000). Similar morphological differences were also detected in parr along a longitudinal river gradient in the Willamette and McKenzie Rivers such that parr in downstream sites had a similar morphology to autumn migrants and parr in the upstream site had a similar morphology to yearling smolts. While this study did not seek to distinguish between genetic and environmental effects on morphology, these results do suggest that redistribution of fish early in life is associated with differentiation in morphology and with the expression of life-history variation.

Body morphology of juvenile *O. tshawytscha* is strongly affected by differences between habitats (Currens *et al.*, 1989; Hard *et al.*, 1999). Downstream sections of

(a)

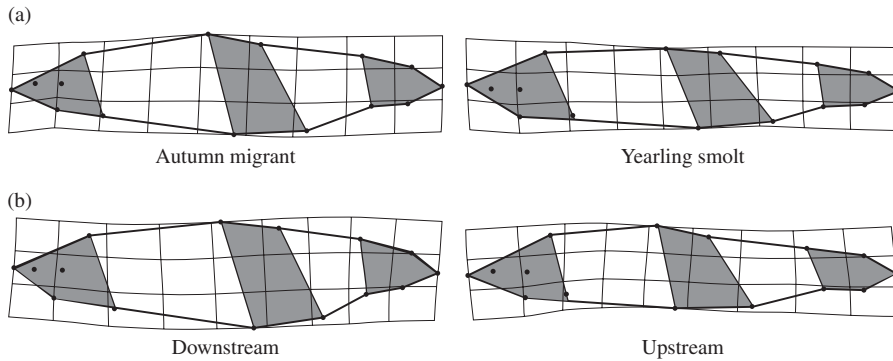Autumn migrant · Yearling smolt

(b)

Downstream · Upstream

FIG. 4. Thin-plate spline transformations depicting morphological differences between *Oncorhynchus tshawytscha* (a) migrants and (b) parr in the Willamette River, Oregon, U.S.A. Transformations were magnified ×3 to better illustrate differences. For the parr analysis, the two downstream sites, *i.e.* Willamette-Harrisburg and lower McKenzie, were combined and represented as a single downstream group.

the upper Willamette River basin (*i.e.* Willamette River and lower sections of major tributaries) have lower gradient and warmer water temperatures compared with upper river sections (monthly mean $\pm$ s.d. summer temperatures $= 16\cdot4 \pm 1\cdot5$ and $11\cdot7 \pm 0\cdot8°$ C for Willamette River and McKenzie River, respectively). Juveniles in upstream and downstream sections experience different flow regimes that probably create selective pressures contributing to morphological differences. Observed morphological differences in this study between *O. tshawytscha* parr in downstream and upstream sites were similar to differences in other salmonids (Swain & Holtby, 1989; McLaughlin & Grant, 1994; Pakkasmaa & Piironen, 2001) and other disparate fish species (Brinsmead & Fox,

TABLE III. Cross-validation classification results of juvenile *Oncorhynchus tshawytscha* parr by means of a linear discriminant function developed with relative warp scores from a morphometric analysis. Parr were separated into groups based on collection site in the Willamette and McKenzie Rivers (WR, Willamette-Harrisburg; MRL, lower McKenzie site; MRU, upper McKenzie site; in the two-group data set, WR and MRL were combined). The prior probabilities of group membership and κ values are also reported

Actual group	Number classified into each group			Total	% Correct
	WR	MRL	MRU		
Three-group data set					
WR	14	11	1	26	54
MRL	4	38	6	48	79
MRU	1	5	38	44	86
Prior probability	0·2203	0·4068	0·3729		
Two-group data set					
MRU	–	70	4	74	95
MRL	–	6	38	44	86
Prior probability	–	0·6271	0·3729		

2002; Langerhans *et al.*, 2003) rearing in different flow regimes. Juveniles in upstream and downstream locations should also experience different growth rates as a result of environmental differences (*e.g.* temperature differences) that will also affect body morphology (Currens *et al.*, 1989) and life-history variation (Beckman *et al.*, 2007; Perkins & Jager, 2011). Thus, morphological variation associated with life-history variation is probably a result of phenotypic plasticity caused by the environments in which juveniles are rearing in the upper Willamette River basin.

Studies have also demonstrated that body morphology in salmonids exhibiting different life-history tactics is the result of genetic variation. In the Nanaimo River, British Columbia, juvenile *O. tshawytscha* exhibit three life-history types that are distinct morphologically and genetically (Carl & Healey, 1984). Resident and migratory brook trout *Salvelinus fontinalis* (Mitchill 1814) have distinct and heritable morphologies when reared under the same environmental conditions (Varian & Nichols, 2010). Additionally, morphological differences in adult salmonids exhibiting different life-history tactics have also been documented (Hendry & Quinn, 1997). Given that morphology (Carl & Healey, 1984; Wessel *et al.*, 2006) and life-history tactic (Clarke *et al.*, 1992, 1994; Waples *et al.*, 2001) in *O. tshawytscha* are heritable, this suggests that adults may produce juveniles that exhibit a similar morphology and life-history tactic.

Morphological and life-history variation of juvenile *O. tshawytscha* were coupled in the upper Willamette River, with fish that rear in different habitats exhibiting different morphologies and life-history tactics. This pattern is consistent with state-dependent models of life-history variation (McNamara & Houston, 1996; Tomkins & Hazel, 2007) such that the expression of life-history tactics is dependent on the match or mismatch of somatic and physiological thresholds and environmental cues that trigger the onset of migration (*i.e.* smoltification) or maturation (*i.e.* early maturation of males) (Beckman *et al.*, 2007). Juveniles that redistribute and rear in downstream sections of the river experience a match of thresholds and environmental signals and migrate downstream as subyearling smolts or autumn migrants. Juveniles that remain to rear in natal tributaries experience a mismatch in thresholds and environmental cues or are unable to perceive such cues and adopt the yearling smolt life-history tactic. While these patterns are consistent with a state-dependent model, it is evident that match or mismatch of thresholds and environmental cues in *O. tshawytscha* occurs early in life, presumably at emergence when downstream movement of young fish primarily occurs (Beckman *et al.*, 2007; Schroeder *et al.*, 2007; Perkins & Jager, 2011). Thus, it is hypothesized that the factors that drive downstream movement of young fish represent the mechanisms that lead to life-history differentiation, *i.e.* juvenile life-history tactics are established much earlier than the onset of smoltification (Thorpe *et al.*, 1998; Beckman *et al.*, 2007; Perkins & Jager, 2011). Not all fish follow the same life-history tactic after their initial dispersal, but it is contended that decisions to disperse or not at emergence set an individual on an initial trajectory that increases their probability of following subsequent migratory patterns (Schroeder *et al.*, 2007).

The sampling design for this study required the comparison of body shape of fish sampled at different times, thus potentially masking the effects of life-history variation with temporal or seasonal effects. Willamette Falls is the only location in the basin to capture juveniles with a known life-history tactic, but it requires sampling autumn migrants and yearling smolts during different seasons. Similarly, disparate growth rates of parr at the three collection sites required samples to be collected sequentially to minimize the effect of body size on group comparisons. For migrants, seasonal effects

would be manifest in changes in condition factor between autumn migrants that have built up fat reserves during the summer months and yearling smolts that have utilized fat reserves during the winter months (Beckman *et al.*, 2000). For parr, temporal effects would be manifest if there were temporal shifts in food availability. In both comparisons of body shape, the temporal or seasonal effects due to changes in condition factor would be apparent in the body depth of the fish (Currens *et al.*, 1989), which was observed in both comparisons of migrants and parr. The head and caudal peduncle regions of juvenile *O. tshawytscha*, however, are relatively insensitive to body shape changes due to changes in condition factor (Currens *et al.*, 1989). While observed differences in body depth were possibly confounded by temporal or seasonal effects, observed differences in the shape of the head and caudal peduncle were evidences that morphological variation is associated with life-history variation in juvenile *O. tshawytscha*.

In establishing the correlation between morphological and life-history variation of juvenile *O. tshawytscha*, this study suggests that life-history differentiation occurs early, perhaps at emergence as suggested by Beckman *et al.* (2007) and Perkins & Jager (2011). Further studies, both experimental and field based, should investigate the factors that contribute to variation in early dispersal of young fish as well as the contribution of juvenile life-history tactics to recruitment of spawning adults (Miller *et al.*, 2010). To the extent that early dispersal is dependent on environmental conditions, the proportion of juveniles that express each migratory phenotype will be dependent on annual variation in these factors. To maintain life-history variation in the population, management actions in the upper Willamette River basin should enhance habitat quality in the historic rearing habitat in lower portions of the basin, enhance population connectivity between upper and lower portions of the basin and maintain the cues that establish patterns of downstream movement of fry, whether environmental or genetic.

References

Beckman, B. R. & Dickhoff, W. W. (1998). Plasticity of smolting in spring Chinook salmon: relation to growth and insulin-like growth factor-I. *Journal of Fish Biology* **53,** 808–826.

Beckman, B. R., Larsen, D. A., Moriyama, S., Lee-Pawlak, B. & Dickhoff, W. W. (1998). Insulin-like growth factor-I and environmental modulation of growth during smoltification of spring Chinook salmon (*Oncorhynchus tshawytscha*). *General and Comparative Endocrinology* **109,** 325–335.

Beckman, B. R., Larsen, D. A., Sharpe, C., Lee-Pawlak, B. & Schreck, C. B. (2000). Physiological status of naturally reared juvenile spring Chinook salmon in the Yakima River: seasonal dynamics and changes associated with smolting. *Transactions of the American Fisheries Society* **129,** 727–753.

Beckman, B. R., Gadberry, B., Parkins, P., Cooper, K. A. & Arkush, K. D. (2007). State-dependent life history plasticity in Sacramento River winter-run Chinook salmon (*Oncorhynchus tshawytscha*): interactions among photoperiod and growth modulate

smolting and early male maturation. *Canadian Journal of Fisheries and Aquatic Sciences* **64,** 256–271.

Beeman, J. W., Rondorf, D. W. & Tilson, M. E. (1994). Assessing smoltification of juvenile spring Chinook salmon (*Oncorhynchus tshawytscha*) using changes in body morphology. *Canadian Journal of Fisheries and Aquatic Sciences* **51,** 836–844.

Bradford, M. J. & Taylor, G. C. (1997). Individual variation in dispersal behavior of newly emerged Chinook salmon (*Oncorhynchus tshawytscha*) from the Upper Fraser River, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* **54,** 1585–1592.

Brinsmead, J. & Fox, M. G. (2002). Morphological variation between lake- and stream-dwelling rock bass and pumpkinseed populations. *Journal of Fish Biology* **61,** 1619–1638.

Careau, V., Thomas, D., Humphries, M. M. & Réale, D. (2008). Energy metabolism and animal personality. *Oikos* **117,** 641–653.

Carl, L. M. & Healey, M. C. (1984). Differences in enzyme frequency and body morphology among three juvenile life history types of Chinook salmon (*Oncorhynchus tshawytscha*) in the Nanaimo River, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* **41,** 1070–1077.

Clarke, W. C., Withler, R. E. & Shelbourn, J. E. (1992). Genetic control of juvenile life history pattern in Chinook salmon (*Oncorhynchus tshawytscha*). *Canadian Journal of Fisheries and Aquatic Sciences* **49,** 2300–2306.

Clarke, W. C., Withler, R. E. & Shelbourn, J. E. (1994). Inheritance of smolting phenotypes in backcrosses of hybrid stream-type x ocean-type Chinook salmon (*Oncorhynchus tshawytscha*). *Estuaries* **17,** 13–25.

Currens, K. P., Sharpe, C. S., Hjort, R., Schreck, C. B. & Li, H. W. (1989). Effects of different feeding regimes on the morphometrics of Chinook salmon (*Oncorhynchus tshawytscha*) and rainbow trout (*O. mykiss*). *Copeia* **1989,** 689–695.

Dimick, R. E. & Merryfield, F. (1945). The fishes of the Willamette River system in relation to pollution. *Oregon State College Engineering Experiment Station Bulletin Series* **20,** 7–55.

Einum, S., Nislow, K. H., McKelvey, S. & Armstrong, J. D. (2008). Nest distribution shaping within-stream variation in Atlantic salmon juvenile abundance and competition over small spatial scales. *Journal of Animal Ecology* **77,** 167–172.

Groot, G. & Margolis, L. (1991). *Pacific Salmon Life Histories*. Vancouver, BC: University of British Columbia Press.

Hard, J. J., Winans, G. A. & Richardson, J. C. (1999). Phenotypic and genetic architecture of juvenile morphometry in Chinook salmon. *Journal of Heredity* **90,** 597–606.

Hassell, E. M. A., Meyers, P. J., Billman, E. J., Rasmussen, J. E. & Belk, M. C. (2012). Ontogeny and sex alter the effect of predation on body shape in a livebearing fish: sexual dimorphism, parallelism, and costs of reproduction. *Ecology and Evolution* **2,** 1738–1746.

Healey, M. C. (1991). Life history of Chinook salmon (*Oncorhynchus tshawytscha*). In *Pacific Salmon Life Histories* (Groot, C. & Margolis, L., eds), pp. 311–393. Vancouver, BC: University of British Columbia Press.

Hendry, A. P. & Quinn, T. P. (1997). Variation in adult life history and morphology among Lake Washington sockeye salmon (*Oncorhynchus nerka*) populations in relation to habitat features and ancestral affinities. *Canadian Journal of Fisheries and Aquatic Sciences* **54,** 75–84.

Irvine, J. R. (1986). Effects of varying discharge on the downstream movement of salmon fry, *Oncorhynchus tshawytscha* Walbaum. *Journal of Fish Biology* **28,** 17–28.

Langerhans, R. B., Layman, C. A., Langerhans, A. K. A. & DeWitt, T. J. (2003). Habitat-associated morphological divergence in two Neotropical fish species. *Biological Journal of the Linnean Society* **80,** 689–698.

Langerhans, R. B., Layman, C. A., Mona Shokrollahi, A. & DeWitt, T. J. (2004). Predator-driven phenotypic diversification in *Gambusia affinis*. *Evolution* **58,** 2305–2318.

McCormick, S. D. (2013). Smolt physiology and endocrinology. In *Fish Physiology: Euryhaline fishes*, Vol. 32 (McCormick, S. D., Farrell, A. P. & Brauner, C. J., eds), pp. 199–251. New York, NY: Elsevier.

McLaughlin, R. L. & Grant, J. W. A. (1994). Morphological and behavioural differences among recently-emerged brook charr, *Salvelinus fontinalis*, foraging in slow- vs. fast-running water. *Environmental Biology of Fishes* **39,** 289–300.

McNamara, N. M. & Houston, A. I. (1996). State-dependent life histories. *Nature* **380,** 215–221.

Miller, J. A., Gray, A. & Merz, J. (2010). Quantifying the contribution of juvenile migratory phenotypes in a population of Chinook salmon *Oncorhynchus tshawytscha*. *Marine Ecology Progress Series* **408,** 227–240.

Moran, P., Teel, D. J., Banks, M. A., Beacham, T. D., Bellinger, M. R., Blankenship, S. M., Candy, J. R., Garza, J. C., Hess, J. E., Narum, S. R., Seeb, L. W., Templin, W. D., Wallace, C. G. & Smith, C. T. (2013). Divergent life-history races do not represent Chinook salmon coast-wide: the importance of scale in Quaternary biogeography. *Canadian Journal of Fisheries and Aquatic Sciences* **70,** 415–435.

Muir, W. D., Zaugg, W. S., Giorgi, A. E. & McCutcheon, S. (1994). Accelerating smolt development and downstream movement in yearling Chinook salmon with advanced photoperiod and increased temperature. *Aquaculture* **123,** 387–399.

Pakkasmaa, S. & Piironen, J. (2001). Water velocity shapes juvenile salmonids. *Evolutionary Ecology* **14,** 721–730.

Perkins, T. A. & Jager, H. I. (2011). Falling behind: delayed growth explains life-history variation in Snake River fall Chinook salmon. *Transactions of the American Fisheries Society* **140,** 959–972.

Pope, K. L. & Kruse, C. G. (2007). Condition. In *Analysis and Interpretation of Freshwater Fisheries Data* (Guy, C. S. & Brown, M. L., eds), pp. 423–471. Bethesda, MD: American Fisheries Society.

Quinn, T. P. (2005). *The Behavior and Ecology of Pacific Salmon and Trout*. Bethesda, MD: American Fisheries Society.

Reimers, P. E. (1968). Social behavior among juvenile fall Chinook salmon. *Journal of the Fisheries Research Board of Canada* **25,** 2005–2008.

Reimers, P. E. (1971). The length of residence of juvenile fall Chinook salmon in Sixes River, Oregon. PhD Thesis, Oregon State University, Corvallis, OR, USA.

Rohlf, F. J. (2003). *tpsRegr, Shape Regression, Version 1.28*. Stony Brook, NY: Department of Ecology and Evolution, State University of New York at Stony Brook.

Rohlf, F. J. (2010a). *tpsDig, Version 2.16*. Stony Brook, NY: Department of Ecology and Evolution, State University of New York at Stony Brook.

Rohlf, F. J. (2010b). *tpsRelw, Relative Warps, Version 1.49*. Stony Brook, NY: Department of Ecology and Evolution, State University of New York at Stony Brook.

Rohlf, F. J. & Slice, D. E. (1990). Extensions of the procrustes method for the optimal superimposition of landmarks. *Systematic Biology* **39,** 40–59.

Schluchter, M. D. & Lichatowich, J. A. (1977). Juvenile life histories of Rogue River spring Chinook salmon *Oncorhynchus tshawytscha* (Walbaum), as determined by scale analysis. *Information Report Series, Fisheries No. 77-5*. Corvallis, OR: Oregon Department of Fish and Wildlife.

Scott, L. E. & Johnson, J. B. (2010). Does sympatry predict life history and morphological diversifications in the Mexican livebearing fish *Poeciliopsis baenschi*? *Biological Journal of the Linnean Society* **100,** 608–618.

Stein, R. A., Reimers, P. E. & Hall, J. D. (1972). Social interaction between juvenile coho (*Oncorhynchus kisutch*) and fall Chinook salmon (*O. tshawytscha*) in Sixes River, Oregon. *Journal of the Fisheries Research Board of Canada* **29,** 1737–1748.

Swain, D. P. & Holtby, L. B. (1989). Differences in morphology and behavior between juvenile coho salmon (*Oncorhynchus kisutch*) rearing in a lake and its tributary stream. *Canadian Journal of Fisheries and Aquatic Sciences* **46,** 1406–1414.

Swain, D. P., Riddell, B. E. & Murray, C. B. (1991). Morphological differences between hatchery and wild populations of coho salmon (*Oncorhynchus kisutch*): environmental versus genetic origin. *Canadian Journal of Fisheries and Aquatic Sciences* **48,** 1783–1791.

Sykes, G. E., Johnson, C. J. & Shrimpton, J. M. (2009). Temperature and flow effects on migration timing of Chinook salmon smolts. *Transactions of the American Fisheries Society* **138,** 1252–1265.

Taylor, E. B. & McPhail, J. D. (1985). Variation in body morphology among British Columbia populations of coho salmon, *Oncorhynchus kisutch*. *Canadian Journal of Fisheries and Aquatic Sciences* **42,** 2020–2028.

Thomas, W. K., Banks, J. L. & Greenland, D. C. (1969). Effect of yolk sac absorption on the swimming ability of fall Chinook salmon. *Transactions of the American Fisheries Society* **98,** 406–410.

Thorpe, J. E., Mangel, M., Metcalfe, N. B. & Huntingford, F. A. (1998). Modeling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L. *Evolutionary Ecology* **12,** 581–599.

Tiffan, K. F. & Connor, W. P. (2011). Distinguishing between natural and hatchery Snake River fall Chinook salmon subyearlings in the field using body morphology. *Transactions of the American Fisheries Society* **140,** 21–30.

Tiffan, K. F., Rondorf, D. W., Rodney, D. G. & Verhey, P. A. (2000). Identification of juvenile fall versus spring Chinook salmon migrating through the Lower Snake River based on body morphology. *Transactions of the American Fisheries Society* **129,** 1389–1395.

Titus, K., Mosher, J. A. & Williams, B. K. (1984). Chance-corrected classification for use in discriminant analysis: ecological applications. *American Midland Naturalist* **111,** 1–7.

Tomkins, J. & Hazel, W. (2007). The status of the conditional evolutionarily stable strategy. *Trends in Ecology and Evolution* **22,** 522–528.

Varian, A. & Nichols, K. M. (2010). Heritability of morphology in brook trout with variable life histories. *PLoS One* **5,** e12950. doi: 10.1371/journal.pone.0012950

Waples, R. S., Gustafson, R. G., Weitkamp, L. A., Myers, J. M., Johnson, O. W., Busby, P. J., Hard, J. J., Bryant, G. J., Waknitz, F. W., Neely, K., Teel, D., Grant, W. S., Winans, G. A., Phelps, S., Marshall, A. & Baker, B. M. (2001). Characterizing diversity in salmon from the Pacific Northwest. *Journal of Fish Biology* **59,** 1–41.

Webb, P. W. (1984). Body form, locomotion, and foraging in aquatic vertebrates. *American Zoologist* **24,** 107–120.

Wesner, J. S., Billman, E. J., Meier, A. & Belk, M. C. (2011). Morphological convergence during pregnancy among predator and nonpredator populations of the livebearing fish *Brachyrhaphis rhabdophora* (Teleostei: Poeciliidae). *Biological Journal of the Linnean Society* **104,** 386–392.

Wessel, M. L., Smoker, W. W. & Joyce, J. E. (2006). Variation of morphology among juvenile Chinook salmon of hatchery, hybrid, and wild origin. *Transactions of the American Fisheries Society* **135,** 333–340.

Zelditch, M. L., Swiderski, D. L. & Sheets, H. D. (2012). *Geometric Morphometrics for Biologists: A Primer*, 2nd edn. London: Academic Press.

Electronic References

Schroeder, K. R., Kenaston, K. R. & McLaughlin, L. K. (2007). Spring Chinook salmon in the Willamette and Sandy rivers. *Oregon Department of Fish and Wildlife*, *Federal Aid in Fish Restoration*, *Project F-163-R-11/12*, *Salem*. Available at https://nrimp.dfw.state.or.us/CRL/Reports/AnnPro/annual%2006-07_final_web%20v3.pdf/ (last accessed 16 April 2014).

Zakel, J. C. & Reed, D. W. (1984). Downstream migration of fish at Leaburg Dam, McKenzie River, Oregon 1980 to 1983. *Oregon Department of Fish and Wildlife*, *Information Report 84-13*. Available at https://nrimp.dfw.state.or.us/CRL/Reports/Info/84-13.pdf/ (last accessed 16 April 2014).