

## Patterns of migration and residency in coastal cutthroat trout *Oncorhynchus clarkii clarkii* from two tributaries of the lower Columbia River

G. B. ZYDLEWSKI\*†, J. ZYDLEWSKI‡§ AND J. JOHNSON‡

\*U.S. Fish and Wildlife Service, Abernathy Fish Technology Center, 1440 Abernathy Creek Road, Longview, WA 98626, U.S.A. and ‡U.S. Fish and Wildlife Service, Columbia River Fisheries Program Office, 1211 Southeast Cardinal Court., Suite 100, Vancouver, WA 98683, U.S.A.

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Coastal cutthroat trout *Oncorhynchus clarkii clarkii* life-history variants, migration and freshwater residency were monitored using stationary passive integrated transponder (PIT) tag arrays in two tributaries of the Columbia River from 2001 to 2005 (Abernathy Creek, river kilometre, rkm 76) and from 2002 to 2005 (Chinook River, rkm 6). In 2001–2003 and 2002–2003 (Abernathy and Chinook, respectively), 300–500 coastal *O. c. clarkii* were captured in each tributary by electrofishing and implanted with 23 mm PIT tags. PIT arrays monitored movements from the initiation of tagging through the spring of 2005. Rotary screw traps were also operated on both tributaries. In Abernathy Creek, 28% of tagged individuals were observed through either active capture or passive interrogation. Of these, 32% were identified as migrants and 68% were identified as residents. In the Chinook River, 48% of tagged fish were observed subsequent to tagging; 92% of these fish were migrants and only 8% were resident. In both tributaries, a greater proportion of resident fish were in the upper reaches. The majority of migrants (78–93%) moved the spring following tagging. Migrants leaving at age 2+ years tended to grow faster than those that migrated at age 3+ years or residents. Patterns of growth or growth opportunities may influence both patterns of life-history expression and the timing of migration.

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### INTRODUCTION

Although there is a general appreciation for the complexity of the coastal cutthroat trout *Oncorhynchus clarkii clarkii* (Richardson) life history, the species remains the least studied of the north-west Pacific salmonids of North America. There is a lack of comprehensive stock assessment data for this species. The precipitous decline of anadromous *O. c. clarkii* in the lower Columbia River over recent decades

§Author to whom correspondence should be addressed at present address: Maine Cooperative Fish and Wildlife Research Unit, U.S. Geological Survey, University of Maine, Nutting Hall, Orono, ME 04469, U.S.A. Tel.: +1 207 581 2853; fax: +1 207 581 2858; email: jzydlewski@usgs.gov

†Present address: School of Marine Sciences, University of Maine, Libby Hall, Orono, ME 04469, U.S.A.

(Leider, 1997) has underscored the importance of understanding the biological and environmental complexities exhibited by these fish.

Sympatric individuals can be resident or migratory (June, 1981; Johnston, 1982; Trotter, 1997), and the expression of life-history characteristics can change during an individual's lifetime. Resident populations are often found in headwater tributaries above barriers to migration. For those fish that do leave their natal streams, they may remain in fresh water (potomadromous) or enter sea water (anadromous; Tomasson, 1978). Although migrating juveniles are thought to undergo a parr-smolt transformation similar to other salmonids, there are no clear morphological distinctions in fresh water between juveniles that are resident or migratory (Tomasson, 1978; Fuss, 1982), making monitoring and conservation activities difficult.

*Oncorhynchus clarkii clarkii* demographics are not well described and have not been differentiated based on migratory status and life-history expression. In the Columbia River, migrating juvenile fish are 2–3 years old and travel downstream in the spring (Johnston, 1982; Trotter, 1989). Juveniles emigrating from Columbia River tributaries (Chinook River, Mill, Abernathy and Germany Creeks) exhibit rapid, directed seaward movements out of the Columbia River and into the ocean (Zydlewski *et al.*, 2008). The only published information on growth rates of *O. c. clarkii* are backcalculated from scales of fish collected in British Columbia (Cooper, 1970). This analysis was confounded by the inability to distinguish resident from migratory life-history forms. In other species, size at age 1 year has been backcalculated using otoliths (Thériault & Dodson, 2003) or size has been compared at different time periods (during migration for anadromous fish and after the migration for resident fish).

The pattern of partial migration, where migratory and non-migratory individuals are present in a population (Jonsson & Jonsson, 1993), exhibited by *O. c. clarkii* is not unique in *Salmo* and *Oncorhynchus* species and follows patterns observed in brown trout *Salmo trutta* L. (Jonsson, 1985) and brook charr *Salvelinus fontinalis* (Mitchill) (Thériault & Dodson, 2003). Life-history strategies associated with partial migration have been related to trade offs in fitness associated with growth, sex and environmental conditions (Hendry *et al.*, 2004). Evolutionary arguments centre on the potential for growth in a marine environment balanced with survival advantages conferred in fresh water (Gross *et al.*, 1988). A relationship between growth rate in fresh water and tendency to undergo an anadromous migration has been shown for *S. trutta* and *S. fontinalis*. Slower growers at age 1+ year tend to remain in fresh water longer or remain resident (Jonsson, 1985; Thériault & Dodson, 2003). The relationship between growth rate and residency in *O. c. clarkii* is equivocal (Nielsen *et al.*, 2003) but is critical for understanding life-history 'decisions'.

In this study, passive integrated-transponder (PIT) tags were used to monitor movements of individuals (remotely and immediately), identify behavioural patterns (*i.e.* migratory status) and estimate growth rates over 5 years. Individual migratory behaviour and freshwater use (anadromy *v.* residency) were examined to compare the growth history of individuals with different migratory status.

## MATERIALS AND METHODS

### FISH CAPTURE AND TAGGING

In October 2001, 2002, and 2003, a 10.5 km section of Abernathy Creek, upstream of the U.S. Fish and Wildlife Service (USFWS), Abernathy Fish Technology Center (Longview, WA, U.S.A.) was sampled (Fig. 1B). In the autumn of 2002 and 2003, a 3.5 km stretch of the Chinook River was sampled upstream of the Sea Resources facility (Chinook, WA, U.S.A.; Fig. 1A). Each tributary was subjectively divided into three sampling reaches; 'lower', 'middle' and 'upper'. For Abernathy Creek, these were river kilometres (rkm) 6.2–8.9, 9.0–11.5 and 11.7–16.7; for the Chinook River these were rkm 6.0–6.9, 7.0–7.9 and 8.0–9.5.

Capture and tagging was carried out in a manner consistent with the conservation goals and fish handling standards of the USFWS. Sampling consisted of electrofishing to capture *O. c. clarkii* >100 mm fork length ( $L_F$ ). Once captured, fish were anaesthetized with 25 ppm clove oil, measured for  $L_F$  and mass ( $M$ ), and a scale sample was taken from the left side. All fish were scanned for previous tagging. A 23 mm previous long, 3.84 mm diameter, 0.6 g; full duplex, PIT tag (Destron Fearing; www.destronfearing.com) was implanted surgically into newly captured fish. A 3 mm incision was made using a sterilized scalpel blade and the tag was inserted manually. The wound was then swabbed with Providine (buffered iodine). Fish were allowed to recover in a tank with flow-through stream water. No mortality was observed as part of the tagging process. All fish were released within 100 m of capture once they recovered from the sampling procedures (usually within 30–60 min of tagging). All release sites were upstream of antenna arrays.

### AGE DETERMINATION

Scales were placed onto adhesive scale cards at the time of sampling for storage. Scales were pressed onto acetate and read using a microfiche projector. Two independent readers aged each scale; if ages differed, a third person read the scale. If there was consensus between two readers, that age value was used. If agreement among readers was not achieved, an age

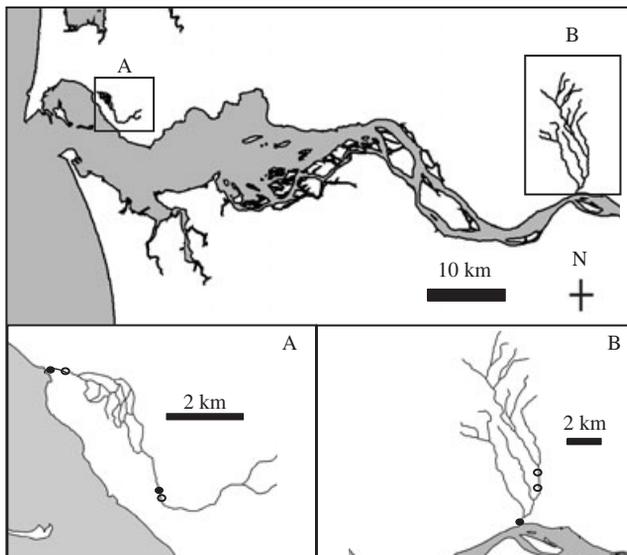


FIG. 1. The lower Columbia River and tributaries monitored for juvenile *Oncorhynchus clarkii clarkii* patterns of migration and residency. Insets A and B depict the Chinook River and Abernathy Creek, respectively. ●, screw trap locations; ○ passive integrated transponder array locations.

was not recorded for the individual. Age could not be determined for all of the samples because many scales were unreadable or regenerative. In particular, many of the scales of the larger fish could not be used because of the high incidence of regeneration as reported by Cooper (1970) for *O. c. clarkii* scales.

## REMOTE DETECTION: STATIONARY PIT ARRAYS

Streamwidth PIT-tag interrogation arrays were used to monitor downstream movement of PIT-tagged *O. c. clarkii* in both tributaries. The stationary detection system monitored the entire width and depth of the streams for PIT-tagged fish, even under high water conditions (Zydlewski *et al.*, 2006). Detection range off the plane of the antennas could be  $\geq 600$  mm or more, but varied with environmental conditions (Zydlewski *et al.*, 2003). This provided continuous (year-round at a 50 ms resolution) monitoring past a single point in a stream without obstructing the path of the fish.

Antennas were constructed using open-coil inductor loops with multistrand wire strung through a PVC pipe. The readers, power supplies and PCs necessary to collect and record data were placed in weather-proof boxes near the sites. Data collected from these sites included PIT code and time of detection. All detections were recorded and uploaded with the Pacific States Marine Fisheries Commission (PSMFC) database PTAGIS. Detection histories for all individuals were downloaded from the PSMFC website. Detection histories were used to report migration timing and determine migratory status.

Abernathy Creek, a third-order tributary of the Columbia River, is *c.* 17 km in length. The stream has a moderately high gradient, dominated by pools and riffles, entering the Columbia River at rkm 76. Tidal influence is restricted to the area near this confluence. Two antenna arrays were installed at *c.* rkm 3 and 4 (Fig. 1), both spanned the total width of the stream. The upper array comprised three independent antennas and the lower array comprised two individual antennas. The construction of both these arrays was completed on 1 October 2001 and they were operated continuously (with short breaks due to damage from high-flow events) during the length of the study. The sequential arrangement of these arrays provided directional information for migrating fish. Through the period of operation, the combined detection efficiency (the proportion of tags known to have transitioned through the stream that were detected by at least one array of antennas) of the arrays was estimated as 83–97% (Zydlewski *et al.*, 2006).

The Chinook River, a second-order tributary, is *c.* 10 km in length. It has a low gradient, tidal system that experiences tidal influence several kilometres from its confluence with the Columbia River at rkm 6 of the Columbia River. Above tidal influence, the tributary is dominated by long pools with slow moving water. The upper reaches are heavily affected by beaver *Castor canadensis* activity. Tidal effects are moderated from historic fluctuations by the presence of tide gates at the mouth of the tributary. Two antenna arrays were constructed at rkm 0 and 6. The upper array was above tidal influence and operated continuously from September 2002 through to the end of this study. This array comprised two sequential antennas (*c.* 15 m apart) that each completely spanned the river, affording directional information at this site. These antennas have a calculated read efficiency of 100% (no 23 mm tag has been read on one antenna and missed on the other). The lower array had three antennas (in tide gate slots), which span the entire river near the confluence with the Columbia River. Because of fluctuating salinity (ranging from 0 to 17), this site experiences poor read range due to electrical loading. The site was manipulated between 2002 and 2005 to increase read range. Detection efficiencies (based on drone tags), however, varied between 10 and 99% over time due to tidal conditions.

## RECAPTURE: SCREW TRAP

Screw traps were operated in both tributaries, making physical recapture of PIT-tagged fish possible. On Abernathy Creek, Washington Department of Fish and Wildlife operated a 2 m screw trap from *c.* 1 April to 30 June each year from 2001 to 2005 at rkm 1 [Fig. 1(b) and 2]. On the Chinook River, Sea Resources, Inc., operated two screw traps year-round [with some interruptions for maintenance; Fig. 1(a) and 3]. A 1.5 m trap was located immediately

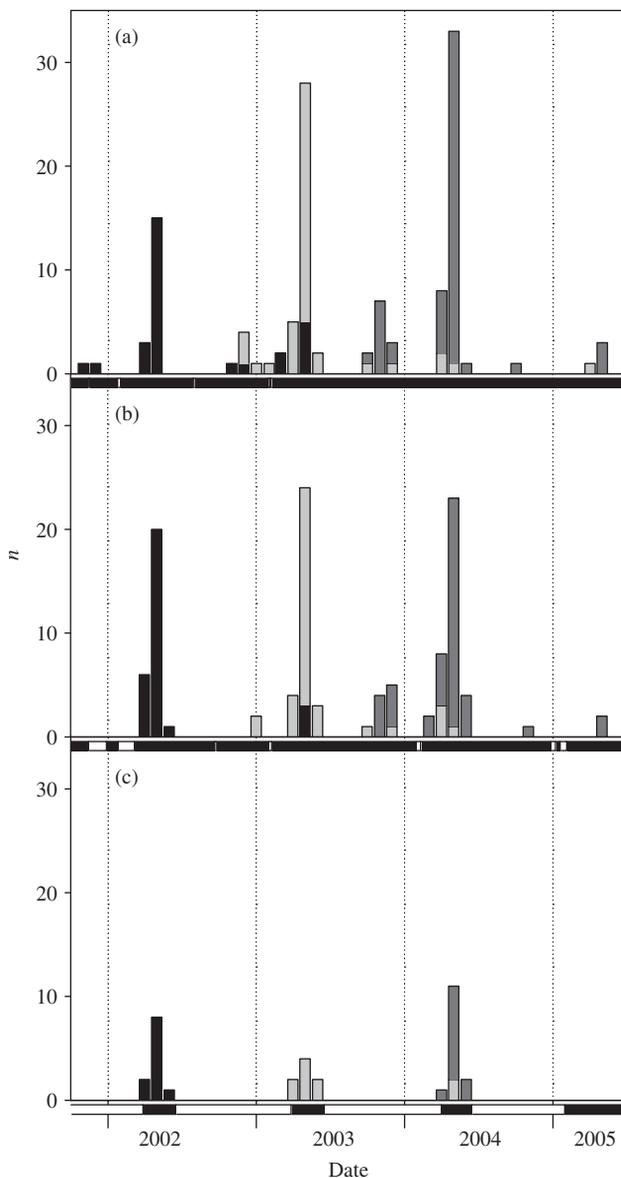


FIG. 2. Migration timing of juvenile *Oncorhynchus clarkii clarkii* from Abernathy Creek. Values are the monthly total number ( $n$ ) of passive integrated-transponder (PIT)-tagged fish tagged in 2001 (■), 2002 (□, light grey) and 2003 (■, dark grey) detected by PIT arrays (a) upper and (b) lower or (c) recaptured by screw trap from October 2001 to June 2005. Horizontal bars beneath each panel represent times of operation (—) for recapture method.

downstream of the antennas of the upper PIT array ('hatchery screw trap') and was actively turned with a motor. A 2 m screw trap was located immediately downstream of the lower PIT array ('mouth screw trap'). When recaptured at the screw traps, PIT-tagged fish were measured, weighed, PIT-tag number recorded, and released below the traps.

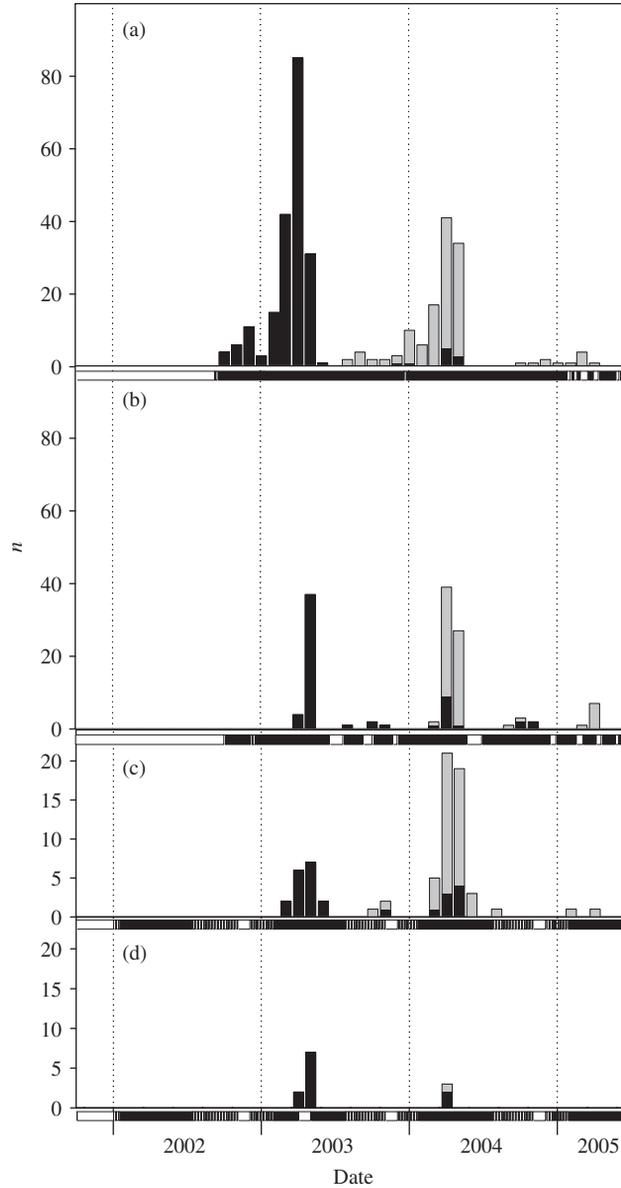


FIG. 3. Migration timing of juvenile *Oncorhynchus clarkii clarkii* from the Chinook River. Values are the monthly total number of passive-integrated transponder (PIT)-tagged fish tagged in 2002 (■) and 2003 (□, grey) detected by PIT arrays (a) upper and (b) lower or recaptured by screw traps (c) hatchery and (d) mouth from October 2001 to June 2005. Horizontal bars beneath each panel represent times of operation (—) for recapture method.

## REMOTE DETECTION: PITPACK

PIT-pack surveys were conducted in Abernathy Creek subsequent to the spring smolt migration (as qualitatively indicated by capture at the screw trap). Two surveyors carrying portable PIT-packs surveyed the stream from the location of the screw trap upstream to the

headwaters. PIT-pack survey efficiencies for Abernathy Creek have been estimated at 38% (Hill *et al.*, 2006). All PIT-tag codes were recorded and used to indicate those individuals remaining in the study area. This method did not, however, allow for physical characteristics of the fish to be measured.

## RECAPTURE: ELECTROFISHING

Physical recaptures were made using electrofishing. Autumn electrofishing efforts in years after initial tagging (2001 in Abernathy Creek and 2002 in the Chinook River) represented opportunities for physical recapture of previously PIT-tagged fish still residing in the tributaries. Electrofishing survey efficiencies are similar to those for PIT-packing (Hill *et al.* 2006). All electrofished individuals were scanned for a PIT tag. Those that were previously tagged were anaesthetized and sampled as above except that a scale sample was taken from the right side of the fish. All fish were released back into their reach (within 100 m) of capture once they recovered from sampling.

## DEFINING MIGRATORY STATUS: 'MIGRANT' AND 'RESIDENT'

Any fish recaptured in a screw trap or detected on a PIT array (downstream of their location of capture and tagging) were classified as migrants. Due to the close proximity between the lowermost electrofishing site and the upper PIT arrays in both Abernathy Creek and Chinook River, only those fish detected 30 days, post-tagging were considered migrants (any movement <30 days post-tagging was considered a potential response to the tagging procedure).

Physical recaptures during electrofishing in the autumn following initial capture were temporarily classified as 'resident'. Also, in Abernathy Creek, all individuals detected with PIT-packs were temporarily classified as 'resident' (all individuals documented during PIT-packing remained as residents). In either case, if a 'resident' fish was subsequently recaptured in a screw trap or detected on a PIT array, the individual fish was reclassified as 'migrant'. In Abernathy Creek, two previously tagged individuals were recaptured by electrofishing 1 year after tagging and subsequently migrated the following spring. There were 11 previously tagged individuals recaptured by electrofishing 1 year after tagging in the Chinook River that migrated the following spring. Fish not detected or physically recaptured subsequent to tagging were classified as having 'unknown' histories. Sources for this category could represent mortalities or inefficiencies in detection and recapture methods.

## GROWTH OF MIGRANTS AND RESIDENTS

Growth of *O. c. clarkii* was retrospectively analysed for all fish that were tagged initially as age 1+ year juveniles and physically recaptured subsequent to tagging (either *via* screw trap or electrofishing). Juveniles tagged as 1+ years that moved the following spring after tagging were defined as migrants moving as 2+ year juveniles (MIG2). Those that waited an additional spring to migrate were defined as migrants moving as 3+ year juveniles (MIG3). As above, those that remained in fresh water for >2 years were defined as resident (RES; Thériault & Dodson, 2003).

For each fish, specific growth rate in mass ( $g_M$ ) was calculated as:  $g_M = (\ln M_2 - \ln M_1) / (t_2 - t_1)^{-1}$ , where  $M_1$  is mass at time of tagging ( $t_1$ ) and  $M_2$  is mass at time of recapture ( $t_2$ ).

## STATISTICS

All statistical differences are reported at the  $P < 0.05$  level. For growth and size analysis ( $L_F$  and  $M$ ) where assumptions were met, a two-way ANOVA was conducted using year and defined migratory status (RES, MIG2 and MIG3) as factors. Migratory status was compared in three ways for  $g_M$ : (1) differences between migrants (leaving any year) or residents regardless

of age at tagging, (2) differences among MIG2, MIG3 or RES for fish age 1+ years at tagging and (3) migrant (MIG2 and MIG3 combined) *v.* RES (all 1+ years at tagging). Differences in  $g_M$  among reaches were compared using a three-way ANOVA on ranked data, with reach, migratory status and year as factors. Significance of factors or interactions was followed by Bonferroni *post hoc* analysis. If data did not meet assumptions for parametric analysis, Kruskal–Wallis analysis was applied. Significance was followed by Dunn's *post hoc* analysis. For each tributary, the proportion of migrants, residents and unknowns were compared for the lower, middle and upper sites using a  $\chi^2$  test. Differences in these proportions between the tributaries were also examined using a  $\chi^2$  test on proportions pooled for all years. All means are reported as mean  $\pm$  s.e.

## RESULTS

### TAGGING: ABERNATHY CREEK

A total of 1496 *O. c. clarkii* >100 mm were PIT tagged between October 2001 and November 2003 in Abernathy Creek (Table I). The  $L_F$  of tagged fish ranged from 100 to 352 mm. Values of  $L_F$  and  $M$  did not differ among years (Table I). The majority (76%) of tagged fish were age 1+ year juveniles (153 of 648, 24%, of aged individuals were aged >2+ years at tagging). Fish determined to be 1+ years were smaller in  $L_F$  and  $M$  than older fish ( $P < 0.001$ ). No statistical difference in  $L_F$  or  $M$  was detected between age 2+ and 3+ year fish. Differences in size at ages 2 and 3 years, however, are, probably due to the low sample size of age 3+ year fish captured. The age structure at tagging did not differ among years.

### TAGGING: CHINOOK RIVER

A total of 754 *O. c. clarkii*  $L_F$  100–293 mm were PIT tagged between October 2002 and November 2003 in the Chinook River (Table I). The  $L_F$  at tagging did not differ among years but  $M$  at tagging was significantly greater in 2002 ( $P < 0.05$ ). The majority (79%) of tagged fish were 1+ year juveniles (108 of 507, 21%, of aged individuals were aged >2+ years at tagging). Fish determined to be 1+ years were smaller in  $L_F$  and  $M$  than older fish trout ( $P < 0.001$ ). Differences in age structure at tagging were detected from 2002 to 2003, with more young-of-the-year (YOY; age 0 years) being tagged in 2003 ( $P < 0.001$ ).

### RECAPTURE HISTORY

The proportions of *O. c. clarkii* defined as migrant or resident differed in the two tributary streams sampled ( $P < 0.001$ ). Of the fish encountered after tagging in Abernathy Creek, 32% (9% of total) were defined as migrants and 68% (19% of total) as residents (Fig. 4). In the Chinook River, 91% of the fish observed were defined as migrants (52% of total), whereas 8% (4% of total) were defined as residents (Fig. 5). The percentage of fish that were not observed subsequent to tagging differed between systems; in Abernathy Creek, 72% of all tagged fish were not detected (unknown), whereas in the Chinook River fewer (52% of all tagged fish) were not observed. These recapture rates are comparable with other mark–recapture studies of salmonids (*e.g.* 30–58%, Budy *et al.*, 2007; 22–31%, Brakensiek & Hankin, 2007).

TABLE I. Size (fork length,  $L_F$ , and mass,  $M$ ) and age of *Oncorhynchus clarkii clarkii* tagged in Abernathy Creek (2001–2003) and the Chinook River (2002–2003) WA. Values are median, with range in parentheses

Year	Age (years)	Size of tagged fish			Abernathy Creek			Chinook River		
		$n$	$L_F$ (mm)	$M$ (g)	$n$	$L_F$ (mm)	$M$ (g)	$n$	$L_F$ (mm)	$M$ (g)
2001	0	—	—	—	—	—	—	—	—	—
	1	14	124 (103–179)	18.3(10–44)	—	—	—	—	—	—
	2	3	135 (113–144)	21.9(14–27)	—	—	—	—	—	—
	3	0	—	—	—	—	—	—	—	—
	All	469	137 (100–390)	24.3(9–680)	—	—	—	—	—	—
2002	0	—	—	—	—	—	—	—	—	—
	1	239	120 (101–254)	16.2(10–211)	2	103 (102–103)	10.1(10–11)			
	2	56	157 (113–259)	36.2(14–165)	250	126 (102–279)	18.7(8–14)			
	3	3	246 (197–352)	140.1(69–432)	60	157 (111–293)	34.5(13–232)			
	All	494	137 (100–352)	24.0(10–432)	5	226 (192–250)	118.1(76–131)			
2003	0	—	—	—	444	131 (102–293)	20.9(7–232)			
	1	239	123 (101–246)	17.7(9–138)	44	111 (101–136)	13.3(10–23)			
	2	84	166 (123–286)	42.0(21–230)	103	125 (103–161)	17.8(9–160)			
	3	10	233 (216–312)	132.6(100–305)	36	148 (115–197)	29.1(15–60)			
	All	533	138 (101–316)	24.9(9–320)	7	218 (179–250)	87.7(40–134)			
					310	130 (100–250)	19.2(9–160)			

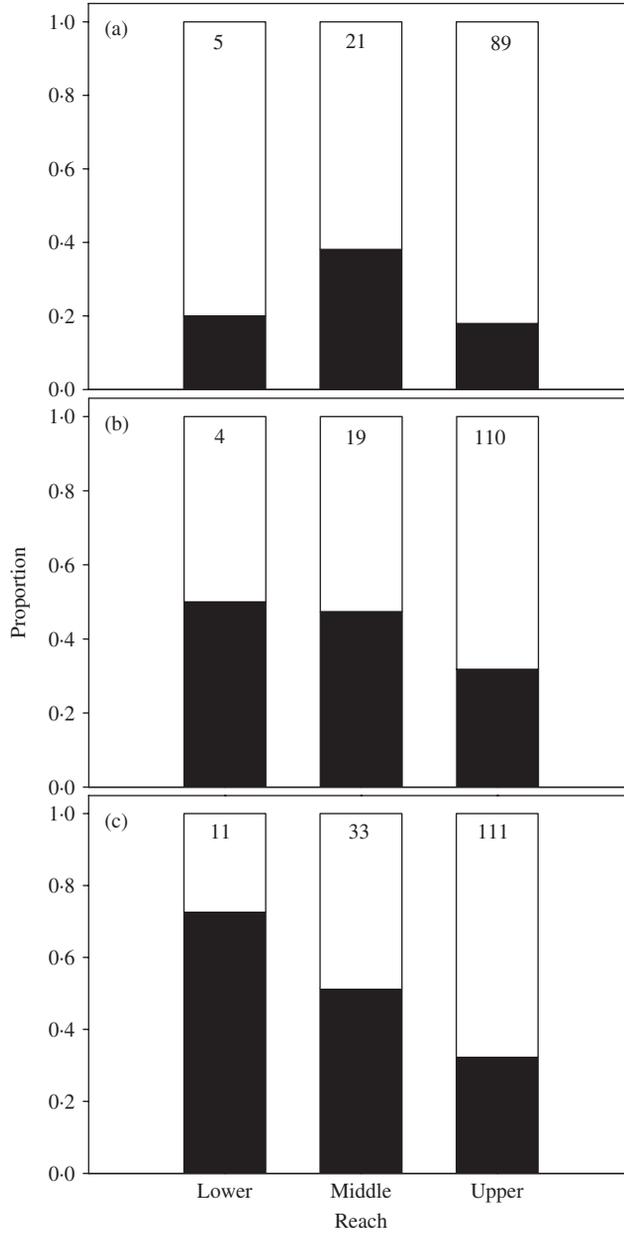


FIG. 4. Proportion of juvenile *Oncorhynchus clarkii clarkii* classified as migrant (■) and resident (□) in Abernathy Creek in lower, middle and upper reaches for (a) 2001, (b) 2002 and (c) 2003. Numbers within bars are the total number of individuals with known histories in each reach.

Size at tagging of ‘unknown’ and ‘known’-history individuals differed for Abernathy Creek and Chinook River fish. For the Chinook, there was no difference in size at tagging between those with known and unknown histories. Therefore, the Chinook residents and migrants represent an unbiased sub-sample of the population.

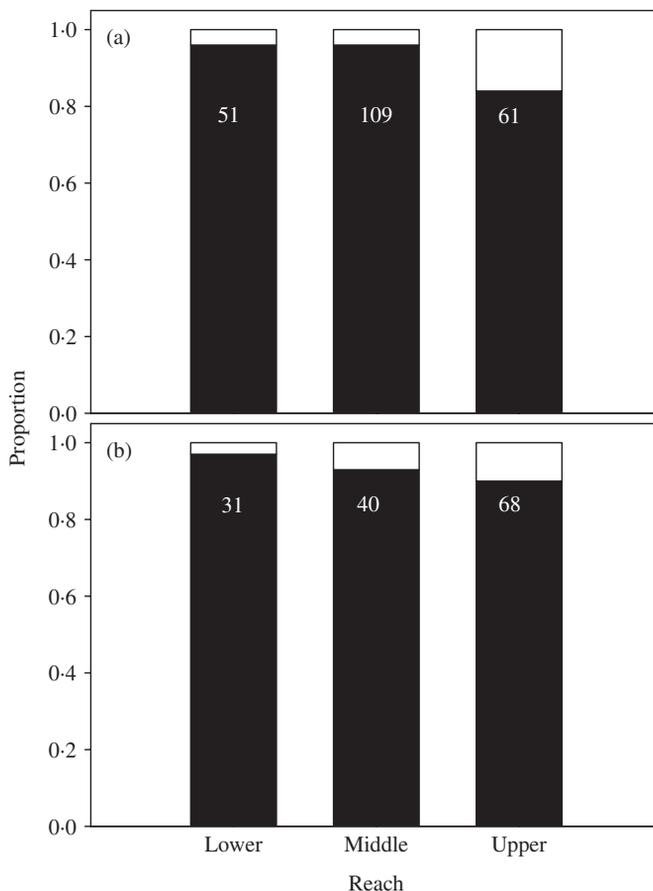


FIG. 5. Proportion of juvenile *Oncorhynchus clarkii clarkii* classified as migrant (■) and resident (□) in the Chinook River in lower, middle and upper reaches for (a) 2002 and (b) 2003. Numbers within bars are the total number of individuals with known histories in each reach.

For Abernathy Creek, the size of the unknown-history individuals at tagging was significantly larger ( $L_F$  but not  $M$ ) than those with known histories.

In both tributaries, the proportion of the various life-history types (*i.e.* migrant, resident and unknown) varied among reaches, although among reach variation was less pronounced (or not detected) when examining these data within years. In Abernathy Creek, the proportion of migrants, residents and unknown varied by reach ( $P < 0.01$ ) for all years, but this relationship was only significant for 2003 ( $P < 0.05$ ) when proportions were compared within years. Power of analysis, however, was low for 2001 and 2002 (power = 0.235 and 0.352, respectively). In the Chinook River, the proportion of migrants, residents and unknown history also varied by reach ( $P < 0.001$ ) when all years were combined though the relationship was significant for 2002 ( $P < 0.01$ ) but not for 2003 ( $P > 0.05$ ).

When considering only the individuals with defined histories (omitting unknowns), the proportion of migrants increased from upper to lower sites in both tributaries (Figs 4 and 5). For Abernathy Creek, this difference is significant when all years are

combined ( $P < 0.01$ ) and in 2003 ( $P < 0.01$ ), but not in 2001 and 2002. Similarly, in the Chinook River, this trend was significant when 2002 and 2003 data were combined and for 2002 ( $P < 0.01$ ) but not for 2003.

## MIGRANTS

The majority of migrating fish emigrated in the year following tagging in both systems. In Abernathy Creek, this amounted to 78, 85 and 93% of observed migrants tagged in 2001, 2002 and 2003, respectively. Similarly, in the Chinook River, 88 and 92% of observed individuals migrated the following year after tagging in 2002 and 2003, respectively. This included individuals tagged at age 0+ year. In 2002, two of two 0+ year fish tagged migrated in April 2003. Of the 44 aged 0+ years tagged in 2003, 13 migrated in April to May 2004, two were later verified as residents and 29 had unknown histories. For all fish (Abernathy Creek and Chinook River) tagged as 1+ years, a minority migrated in the second year after tagging and only one fish was observed in Abernathy Creek migrating in the third.

In both Abernathy Creek and the Chinook River, there was a clear peak in movement from May to July (Figs 2 and 3). In the months of November to January, there was a second peak of less magnitude observed in both systems. The peak of movement in Abernathy Creek was more than a month earlier than the peak observed in the Chinook River.

Patterns of movement between the upper and lower array towards its confluence with the Columbia River differed between the two systems. In Abernathy Creek, the peak of movements at the upper array, lower array and screw trap on Abernathy Creek all occurred within days of each other. In the Chinook River, the peak of movement past the upper array in late April was off set by *c.* 2 weeks from the lower site. Although there was a clear peak of downstream movement at the upper site, downstream movements from August 2002 to March 2003 accounted for nearly one third of all observed movements. The timing of exit into the Columbia River subsequent to moving past the upper site was quite varied (Fig. 3). The majority of fish moved past the second antenna (a distance of some 5 km) in <60 days, but nearly 25% of the fish remained in the lower part of the Chinook River system for 3–10 months.

## SIZE AND GROWTH OF FISH TAGGED AS 1+ YEARS

Size at tagging of fish tagged as 1+ year juveniles differed based on defined migratory status group (MIG2, MIG3 or RES) but not among years in both Abernathy Creek and the Chinook River. In Abernathy Creek, both  $L_F$  and  $M$  were significantly different among migratory status groups at tagging (both  $P < 0.01$ ). For both  $L_F$  and  $M$ , MIG2 were significantly greater *v.* either those observed as MIG3 or as RES [Fig. 6(a) and (c)]. In the Chinook River, both  $L_F$  and  $M$  were significantly different among migratory status groups at tagging (both  $P < 0.001$ ). For both  $L_F$  and  $M$ , MIG2 were significantly greater *v.* either those observed as MIG3. In contrast to observations in Abernathy Creek, RES did not differ from either MIG2 or MIG3 [Fig. 6(b) and (d)].

Differences between migratory status groups corresponded to differences in calculated specific growth rate ( $g_M$ ). Year of study was not a significant factor for

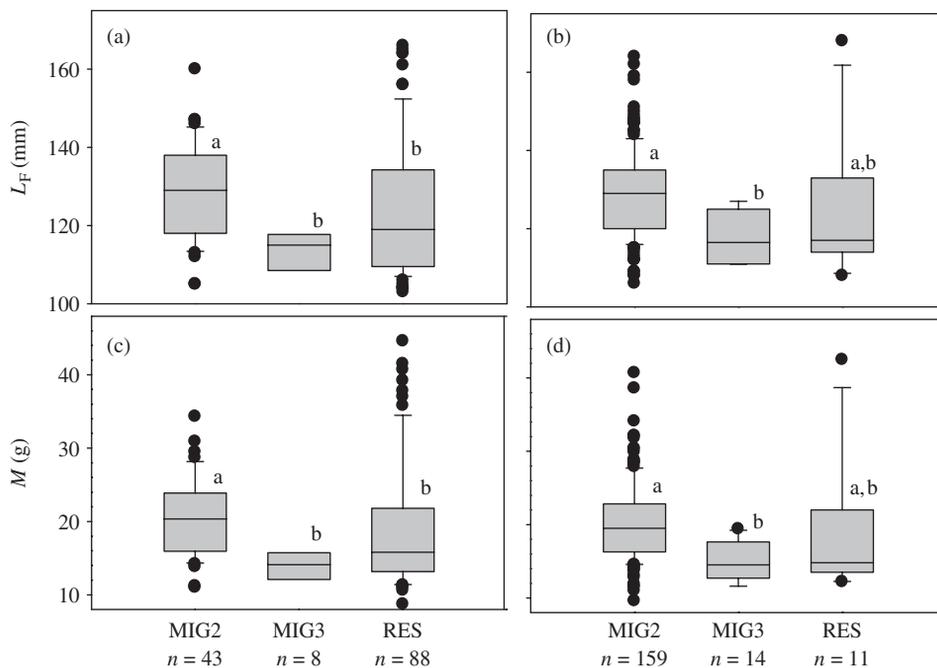


FIG. 6. Box plots of (a), (b) fork length ( $L_F$ ) and (c), (d) mass ( $M$ ) of *Oncorhynchus clarkii clarkii* tagged as 1+ year juveniles in (a), (c) Abernathy Creek and (b), (d) the Chinook River observed migrating as 2+ years (MIG2), migrating as 3+ years (MIG3) or as residents (RES). The end of each box define the 25th and 75th percentiles, the line within the box is the median, the error bars (whiskers) denote the 10th and 90th percentiles, with the outliers represented by ●. Those with the same lower case letters were not statistically different ( $P > 0.05$ ).

either tributary. In Abernathy Creek, MIG2 fish had a  $g_M$  that was 50% greater than RES fish [ $0.335 \pm 0.034$  and  $0.222 \pm 0.014$ , respectively; Fig. 7(a)]. Neither MIG2 nor RES differed from MIG3 ( $0.262 \pm 0.014$ ), however, only two fish satisfied the criteria for this category. When pooled, migrants of original age 1+ years (MIG2 and MIG3) had a  $g_M$  value that was 48% greater than RES ( $0.324 \pm 0.029$ ,  $n = 9$  and  $0.219 \pm 0.014$ ,  $n = 46$ , respectively;  $P < 0.01$ ). When all tagged fish were included (tagging ages of 0+, 1+, 2+ and 3+ years), the  $g_M$  of fish categorized as migrants remained higher than residents but with a lesser magnitude ( $0.272 \pm 0.005$  g,  $n = 33$  and  $0.217 \pm 0.009$ ,  $n = 127$ , respectively;  $P < 0.001$ ).

Although a similar trend was observed in the Chinook River, the  $g_M$  of MIG2 fish did not differ significantly from RES fish at the  $P = 0.05$  level ( $0.447 \pm 0.020$  and  $0.339 \pm 0.041$ , respectively). The value of  $g_M$  of MIG2 fish was, however, 62% higher than that of MIG3 [ $0.447 \pm 0.020$  and  $0.276 \pm 0.049$ , respectively; Fig. 7]. The value of  $g_M$  of RES fish did not differ from MIG3. When pooled, the  $g_M$  of migrants tagged at age 1+ years (MIG2 and MIG3) did not differ from RES ( $0.417 \pm 0.044$ ,  $n = 44$  and  $0.339 \pm 0.041$ ,  $n = 11$ , respectively;  $P > 0.05$ ). When all tagged fish were included (tagged at ages of 0+, 1+, 2+ and 3+ years), however, the  $g_m$  of migrants was 41% greater than that of residents ( $0.416 \pm 0.013$ ,  $n = 90$

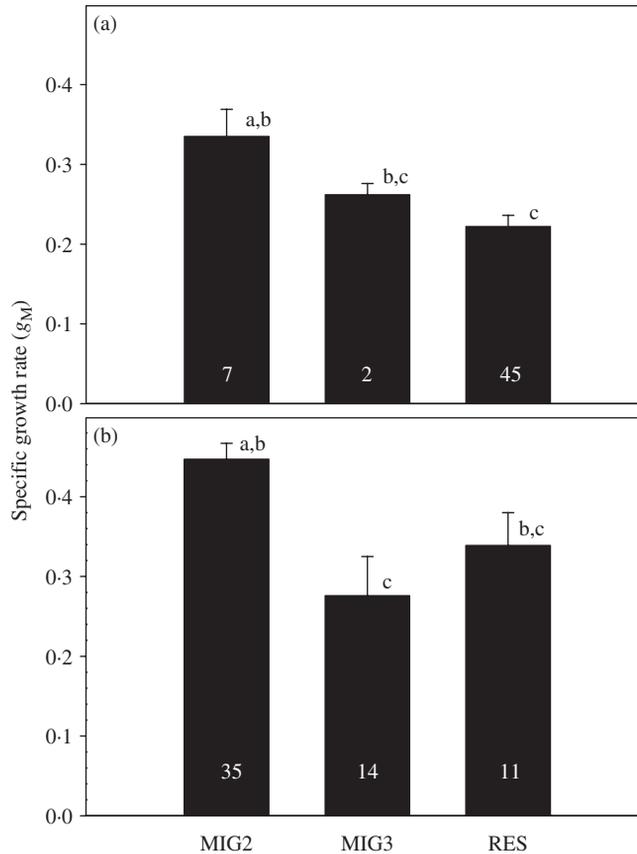


FIG. 7. Specific growth in mass ( $g_M$ ) of *Oncorhynchus clarkii clarkii* tagged as 1+ year juveniles in (a) Abernathy Creek and (b) the Chinook River observed as migrants (as 2+ years, MIG2, or as 3+ years, MIG3) or residents (RES) and physically recaptured (by electrofishing or screw trapping). Means with the same lower case letters are statistically similar ( $P > 0.05$ ). Numbers in bars indicate number of fish in each group.

and  $0.295 \pm 0.024$ ,  $n = 27$ , respectively;  $P < 0.001$ ). There were no differences in  $g_M$  among tributary reaches in the Chinook River or Abernathy Creek.

## DISCUSSION

*Oncorhynchus clarkii clarkii* in Abernathy Creek and Chinook River were of similar age and size with the predominant age class available for capture in the autumn of the 3 years of tagging being 1+ years. The  $L_F$  averaged 120–125 mm and  $M$  averaged 16.2–18.7 g for age 1+ year individuals. The majority of downstream migration observed in both tributaries occurred in the spring. The peak of juvenile emigration from both tributaries occurred from March to June (primarily April and May; Figs 2 and 3) each year. Qualitatively, however, the peak time of juvenile emigration from Chinook River (April) was initiated more than a month earlier than

the first observations of downstream migrants in Abernathy Creek (May). Migration timing, percentage of fish migrating in the spring following tagging (78–93%), and age at migration (2+ years) are consistent to those reported for other *O. C. clarkii* populations. Trotter (1989) reported a peak in mid-May for Washington and Oregon populations with the majority of fish migrating at age 2+ years.

Once migration was initiated, patterns of movement between the upper part of these tributaries and their confluence with the Columbia River differed. In Abernathy Creek, once a fish was encountered moving past the upper antenna, movement downstream was rapid and directed; peak movements between upper and lower arrays and the screw trap were nearly coincident. In contrast, movement past the upper antenna in the Chinook River occurred days to weeks in advance of the observed peak at the lower antenna. The timing of the peak at the lower array in the Chinook River, however, was more consistent with that observed in Abernathy Creek (May).

Physical differences between these tributaries (gradient, tidal influence and array placement) may explain differences in movement patterns. In the Chinook River, the lower antenna is close to the confluence with the Columbia River, an area that is heavily influenced by tidal fluctuations and is highly productive. In tidal systems such as the Chinook River, downstream movements from headwater areas may be movements into rearing habitat rather than a seaward migration. Many fish in the Chinook River moved past the upper array between September and March prior to spring emigration the following year. Even those that moved more rapidly downstream spent nearly a month (on average) in the lower part of the tributary. This pattern underscores the potential importance of the lower part of this tidal system as a rearing area.

In Abernathy Creek, the lack of such rearing habitat may explain the relative undistracted nature of *O. c. clarkii* movement towards the Columbia River. The significance of the second peak of movement between November and January (Fig. 2) is less certain in Abernathy Creek. Perhaps, individuals observed moving in the autumn are overwintering in the lower part of the Creek or entering the main-stem of the Columbia River. This distinction would be important when defining potential impacts on *O. c. clarkii* as a result of any anthropogenic disturbance.

Differences in the prevalence of migratory *v.* resident life histories are also observed in these two tributaries. In Abernathy Creek, resident *O. c. clarkii* were observed roughly at a ratio of 2:1 (Fig. 4) in favour of residents. In stark contrast, migrants in the Chinook River outnumbered residents at a ratio of 11:1 (Fig. 5). It should be noted that variability in odds of 'capture' were probably different in each tributary, and different proportions of 'unknown' fish occurred. In Abernathy Creek, 72% of tagged fish were not observed again, whereas this proportion was 52% in the Chinook River. Such differences have the potential of introducing bias; however, the data suggest that size did not influence survival of 'known' and 'unknown' individuals.

*Oncorhynchus clarkii clarkii* with known histories in the Chinook River were similar in size to those with unknown histories. There was a difference in size at tagging of fish among fates in Abernathy Creek; however, those with unknown histories were longer than those with known histories. If tagging resulted in a greater probability of mortality for unrecovered (unknown) individuals, then unknown would have been smaller than known fish.

Differences in efficiencies are likely to add some level of bias to the analyses of resident and migrant proportions. Resident fish in Abernathy Creek had greater probability of being observed because PIT packs were not used in the Chinook River (for logistical reasons). When residents classified with the PITpack in Abernathy Creek are removed from the analysis, the per cent of residents decreases from 19 to 8% (making the ratio of residents to migrants 1:1). Conversely, migrants in the Chinook River had greater probability of being observed because the PIT array in the Chinook River had excellent detection efficiency (indistinguishable from 100%) compared to the arrays on Abernathy Creek which had a net efficiency that ranged from 83 to 97%. This estimate may be conservative; data from the screw trap on Abernathy Creek, however, indicate the antennas recorded 32 of 33 tagged fish (97%). Similarly, 19 of 20 (95%) of PIT tags recovered on Caspian tern *Sterna caspia* and double crested cormorant *Phalacrocorax auritus* colonies in the lower Columbia River were observed at the arrays (G. Zydlewski unpubl. data).

Regardless, these potential biases are not of sufficient magnitude to explain the considerable difference in the ratios of resident and migrant *O. c. clarkii* observed in these two tributaries. The difference may be related to the migratory distances traversed by fish from these tributaries. Because migrants from both Abernathy Creek and the Chinook River have been shown to enter into the Columbia River plume after reaching their respective confluences (Zydlewski *et al.*, 2008) the distance between tributaries (70 km) probably reflects a real difference in distance travelled. There may be a relative advantage to migrants that undergo a shorter movement (in the Chinook River) towards areas of higher productivity (favouring migrants) *v.* survival risks associated with migration (*e.g.* predation).

Such a trade-off may also explain the difference in migrant and resident proportions observed on a smaller scale within each tributary. A greater proportion of tagged individuals in lower sections were observed as migrants (conversely a greater proportion was observed as residents in the upper reaches; Figs 4 and 5). This is consistent with other reports that sea-run *O. c. clarkii* inhabit the lower reaches of tributaries, especially below barriers (Cooper, 1970; Michael, 1983). There was, however, considerable variability and these trends were not significant for each year (however, power of these analyses was low).

It is likely that this within-river cline in migratory status represents a trade-off in survival and the advantages of growth conferred upon successful migrants. This is the first evidence for a clinal variation in life-history strategy in *O. c. clarkii* without an impassable barrier present. Northcote (1997) reviewed the importance of sustaining the migratory and residency spectrum within the *O. c. clarkii* life-history repertoire as a mechanism of 'bet-hedging' in response to the pressures of environmental variability and unpredictability. Residency has been documented as common and pervasive for populations inhabiting inland waters, but has become strongly fixed only for those above-waterfalls.

Integration of techniques in this study allowed physical recapture of individuals with known histories (from PIT tags) at screw traps (migrants) and during electrofishing (residents) for retrospective analysis, including size and growth rates. In general, juvenile *O. c. clarkii* that were destined to migrate the next spring after tagging were larger and had a faster  $g_M$  than resident fish. These comparisons are made complex by the differences in age at tagging as well as the variability in the age at migration. By analysing data for only individuals that were tagged at age 1+

years, it is clear that the growth of *O. c. clarkii* migrating as 2+ years (MIG2) is accelerated relative to residents (in Abernathy Creek) and those that migrate as 3+ years (MIG3) in the Chinook River (Figs 6 and 7).

Size differences within a river have been described in other populations of *O. c. clarkii*, with residents being smaller than anadromous individuals (Sumner, 1962). Individuals migrating from the lower parts of streams have been observed to grow faster than those from upper reaches (Cooper, 1970) and were presumed to be anadromous. The evidence presented here connects these two observations by reporting individual growth rates based on life history and reporting the origin of the juvenile within a catchment. A parallel trend is observed in *S. fontinalis* (Thériault & Dodson, 2003) but has not been directly demonstrated in any *Salmo* or *Oncorhynchus* species.

This study presents the first documented relationship between partial migration and growth of *O. c. clarkii*. Faster growth observed in migrant fish is consistent with life-history theory that greater size in fresh water is advantageous for migration (Jonsson, 1985; Svenning *et al.* 1992). Although evolutionary theory may predict that growth opportunities for non-migrants are lower in fresh water and growth rate should compensate to increase body size for survival and reproduction (Hendry *et al.* 2004), the present evidence is more consistent with the arguments of Jonsson & Jonsson (1993). They suggest that individual fishes will remain in a niche until they approach a certain size when they either mature or switch to a new niche (migrate), with slower growers remaining in fresh water longer or remaining as residents. Based on this, downstream migrants are larger than non-maturing residents and migration selects for fishes in better condition (Jonsson & Jonsson, 1993). It is reasonable, therefore, to hypothesize that changes in growth scope within a habitat may influence the proportion of a population that undergoes migration. Data here support this hypothesis.

Fish in the Chinook River exhibit accelerated growth when compared to fish in Abernathy Creek probably reflecting habitat differences (growth scope). Chinook River resident *O. c. clarkii* grew at nearly the same rate as Abernathy Creek migrants. There is a corresponding difference in residency and migratory behaviour among the streams. Relatively few fish migrate from Abernathy Creek and relatively few fish remain as residents in the Chinook River. Age 0+ year fish in the Chinook River being large enough to tag (>100 mm) and migrating at 1+ years are an excellent example of a habitat with high growth scope and different growth opportunities than Abernathy Creek which has a higher proportion of residents.

Many anadromous populations of *O. c. clarkii* have plummeted in recent years, including those of the Columbia River (Nehlsen *et al.*, 1991; Hooton, 1997; Leider, 1997). In contrast, it has been argued that resident populations have not declined (Washington Department of Fish and Wildlife, unpubl. data). This apparent distinction has been listed as a key deciding issue in the failed petition to list (under the U.S. Endangered Species Act) *O. c. clarkii* the lower Columbia River (Brown & Craig, 2002). Implicated anthropogenic practices such as logging (Holtby, 1987; Johnson *et al.*, 1999) overharvest (Gresswell & Harding, 1997) and artificial propagation (Flagg *et al.*, 1995) may effect *O. c. clarkii* by influencing growth opportunities. Such effects, in turn, could reduce the life-history variation exhibited by *O. c. clarkii* populations.

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### References

- Brakensiek, K. E. & Hankin, D. G. (2007). Estimating overwinter survival of juvenile coho salmon in a northern California stream: accounting for effects of passive integrated Transponder tagging mortality and size-dependent survival. *Transactions of the American Fisheries Society* **136**, 1423–1437.
- Brown, R. & Craig, S. (2002). Department of the Interior Fish and Wildlife 50 CFR Part 17 Endangered and threatened wildlife and plants; withdrawal of proposed rule to list the southwestern Washington/Columbia River distinct population segment of the coastal cutthroat trout as threatened; proposed rule. *Federal Register* **67**, 44934–44961.
- Budy, P., Thiede, G. P. & McHugh, P. (2007). Quantification of the vital rates, abundance, and status of a critical, endemic population of Bonneville cutthroat trout. *North American Journal of Fisheries Management* **27**, 593–604.
- Cooper, E. L. (1970). Growth of cutthroat trout (*Salmo clarki*) in Chef Creek, Vancouver Island, British Columbia. *Journal of the Fisheries Research Board of Canada* **27**, 2063–2070.
- Flagg, T. A., Waknitz, F. W., Maynard, D. J., Milner, G. B. & Mahnken, C. V. (1995). The effect of hatcheries on native coho salmon populations in the lower Columbia River. In *Uses and Effects of Cultured Fishes in Aquatic Ecosystems* (Schramm, H. L. Jr. & Piper, R. G., eds), pp. 366–375. *American Fisheries Society Symposium* **15**.
- Fuss, H. J. (1982). Age, growth and instream movement of Olympic Peninsula coastal cutthroat trout (*Salmo clarki clarki*). Master's Thesis, University of Washington, Seattle, WA.
- Gresswell, R. E. & R. D. Harding. (1997). The role of special angling regulations in management of coastal cutthroat trout. In *Sea-run Cutthroat Trout: Biology, Management, and Future Conservation* (Hall, J. D., Bisson, P. A. & Gresswell, R. E., eds), pp. 151–156. Corvallis, OR: Oregon Chapter of the American Fisheries Society.
- Gross, M. R., Coleman, R. M. & McDowall, R. M. (1988). Aquatic productivity and the evolution of diadromous fish migration. *Science* **239**, 1291–1293.
- Hendry, A. P., Bohlin, T., Jonsson, B. & Berg, O. K. (2004). To sea or not to sea? Anadromy versus non-anadromy in salmonids. In *Evolution Illuminated: Salmon and their Relatives* (Hendry, A. P. & Stearns, S. C., eds.), pp. 93–125. New York: Oxford University Press.
- Hill, M. S., Zydlewski, G. B., Zydlewski, J. D. & Gasvoda, J. M. (2006). Development and evaluation of portable PIT tag detection units: PITpacks. *Fisheries Research* **77**, 102–109.
- Holtby, L. B. (1987). The effects of logging on the coho salmon of Carnation Creek, British Columbia. In *Proceedings of the Workshop: Applying 15 years of Carnation Creek Results* (Chamberlin, T. W., ed.), pp. 159–174. Nanaimo, BC: Pacific Biological Station.

- Hooton, B. (1997). Status of cutthroat trout in Oregon. In *Sea-run Cutthroat Trout: Biology, Management, and Future Conservation* (Hall, J. D., Bisson, P. A. & Gresswell, R. E., eds), pp. 56–57. Corvallis, OR: Oregon Chapter of the American Fisheries Society.
- Johnson, O. W., Ruckelshaus, M. H., Grant, W. S., Waknitz, F. W., Garrett, A. M., Bryant, G. J., Neely, K. & Hard J. J. (1999). Status review of coastal cutthroat trout from Washington, Oregon, and California. *U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-37*.
- Johnston, J. M. (1982). Life histories of anadromous cutthroat with emphasis on migratory behavior. In *Proceedings of the Salmon and Trout Migratory Behavior Symposium* (Brannon, E. L. & Salo, E. O., eds), pp. 123–127. Seattle, WA: University of Washington.
- Jonsson, B. (1985). Life history patterns of freshwater resident and sea-run migrant brown trout in Norway. *Transactions of the American Fisheries Society* **114**, 182–194.
- Jonsson, B. & Jonsson, N. (1993). Partial migration: niche shift versus sexual maturation in fishes. *Reviews in Fish Biology and Fisheries* **3**, 348–365.
- June, J. A. (1981). Life history and habitat utilization of cutthroat trout (*Salmo clarki*) in a headwater stream on the Olympic Peninsula, Washington. Master's Thesis, University of Washington, Seattle, WA.
- Leider, S. A. (1997). Status of searun cutthroat trout in Washington. In *Sea-run Cutthroat Trout: Biology, Management, and Future Conservation* (Hall, J. D., Bisson, P. A. & Gresswell, R. E., eds), pp. 68–76. Corvallis, OR: Oregon Chapter of the American Fisheries Society.
- Michael, J. H. (1983). Life history of anadromous coastal cutthroat trout in Snow and Salmon Creeks, Jefferson County, Washington, with implications for management. *California Fish and Game* **75**, 188–203.
- Nehlsen, W., Williams, J. E. & Lichatowich, J. A. (1991). Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. *Fisheries* **16**, 4–21.
- Nielsen, C., Aarestrup, K., Nørum, U. & Madsen S. (2003). Pre-migratory differentiation of wild brown trout into migrant and resident individuals. *Journal of Fish Biology* **63**, 1184–1196. doi: 10.1046/j.1095-8649.2003.00237.x
- Northcote, T. G. (1997). Why sea-run? An exploration into the migratory/residency spectrum of coastal cutthroat trout. In *Sea-run Cutthroat Trout: Biology, Management, and Future Conservation* (Hall, J. D., Bisson, P. A. & Gresswell, R. E., eds), pp. 20–26. Corvallis, OR: Oregon Chapter of the American Fisheries Society.
- Sumner, F. H. (1962). Migration and growth of the coastal cutthroat trout in Tillamook County, Oregon. *Transactions of the American Fisheries Society* **91**, 77–83.
- Svenning, M. A., Smith-Nilson, A. & Jobling M. (1992). Sea water migration of Arctic charr (*Salvelinus alpinus* L.)—correlation between freshwater growth and seaward migration, based on back-calculation from otoliths. *Nordic Journal of Freshwater Research* **67**, 18–26.
- Thériault V. & Dodson, J. J. (2003). Body size and the adoption of a migratory tactic in brook charr. *Journal of Fish Biology* **63**, 1144–1159. doi: 10.1046/j.1095-8649.2003.00233.x
- Tomasson, T. (1978). Age and growth of cutthroat trout, *Salmo clarki clarki* Richardson, in the Rogue River, Oregon. Master's Thesis, Oregon State University, Corvallis, OR, USA.
- Trotter, P. C. (1989). Coastal cutthroat trout: a life history compendium. *Transactions of the American Fisheries Society* **118**, 463–473.
- Trotter, P. C. (1997). Sea-run cutthroat trout: life history profile. In *Sea-run Cutthroat Trout: Biology, Management, and Future Conservation* (Hall, J. D., Bisson, P. A. & Gresswell, R. E., eds), pp. 7–15. Corvallis, OR: Oregon Chapter of the American Fisheries Society.
- Zydlewski, G. B., Horton, G., Dubreuil, T., Zydlewski, J., Letcher, B. & Casey, S. (2006). Remote monitoring of fish in small streams: a unified approach using PIT tags. *Fisheries* **31**, 492–502.
- Zydlewski, J., Johnson, J., Brunzell, J., Clements, S., Karnowski, M. & Schreck, C. (2008). Seaward migration of coastal cutthroat trout *Oncorhynchus clarkii clarkii* from fow tributaries of the Columbia River. In *The 2005 Coastal Cutthroat Trout Symposium:*

*Status, Management, Biology and Conservation* (Connolly, P. J., Williams, T. H. & Greswell, R. E., eds), pp. 65–74. Portland, OR: Oregon Chapter of the American Fisheries Society.

### **Electronic Reference**

Zydlewski, G. B., Winter, C., McClanahan, D., Johnson, J., Zydlewski, J. & Casey, S. (2003). Evaluation of fish movements, migration patterns, and population abundance with streamwidth PIT tag interrogation systems. *Project Number 2001-01200, 72 electronic pages, (BPA Report DOE/BP-00005464-1)*. [http://www.delta.dfg.ca.gov/crfg/docs/PitTagEval\\_BPA.pdf](http://www.delta.dfg.ca.gov/crfg/docs/PitTagEval_BPA.pdf)