

Marine survival difference between wild and hatchery-reared steelhead trout determined during early downstream migration

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Abstract: We observed large survival differences between wild and hatchery-reared steelhead trout (*Oncorhynchus mykiss*) during the juvenile downstream migration immediately after release, which persisted through adult life. Following a railway spill of sodium hydroxide into the Cheakamus River, British Columbia, a short-term conservation hatchery rearing program was implemented for steelhead. We used acoustic telemetry and mark–recapture models to estimate survival of wild and (or) hatchery-reared steelhead during 4 years of the smolt migration, with both groups released in 2008. After adjusting for estimated freshwater residualization, 7%–13% of wild smolts and 30%–40% of hatchery smolts died in the first 3 km of the migration. Estimated survival from release to ocean entry was 71%–84% for wild fish and 26%–40% for hatchery fish and to exit from the Strait of Georgia system was 22%–33% for wild fish and 3.5%–6.7% for hatchery fish. A calculated 2.3-fold survival difference established during the downstream migration was similar to that after the return of adult spawners, as return rates were 8.0% for wild fish and 4.1% for hatchery fish. Contrary to current understanding, a large proportion of salmon mortality in the smolt-to-adult period, commonly termed “marine mortality”, may actually occur prior to ocean entry.

Résumé : Nous avons observé de grandes différences sur le plan de la survie entre des truites arc-en-ciel (*Oncorhynchus mykiss*) sauvages et issues d'écloseries durant l'avalaison des juvéniles immédiatement après le lâcher, qui persistaient tout au long de la vie adulte. À la suite d'un déversement ferroviaire d'hydroxyde de sodium dans la rivière Cheakamus (Colombie-Britannique), un programme d'élevage en écloserie de courte durée a été mis en œuvre pour cette espèce. Nous avons utilisé la télémétrie acoustique et des modèles de marquage–recapture pour estimer la survie des truites arc-en-ciel sauvages et (ou) élevées en écloserie durant 4 années de la migration des saumoneaux, les deux groupes ayant été lâchés en 2008. Après ajustement pour tenir compte de la résidualisation en eau douce, il a été établi que 7–13 % des saumoneaux sauvages et 30–40 % des saumoneaux issus d'écloseries étaient morts dans les premiers 3 km de la migration. Le taux de survie estimé du lâcher à l'entrée en mer était de 71–84 % pour les poissons sauvages et de 26–40 % pour les poissons issus d'écloseries, et à la sortie du réseau du détroit de Georgia, de 22–33 % pour les poissons sauvages et 3,5–6,7 % pour les poissons issus d'écloseries. Une différence calculée du simple au double (2,3 fois) établie pour l'avalaison était semblable à la différence établie pour le retour des géniteurs adultes, les taux de retour étant de 8,0 % pour les poissons sauvages et de 4,1 % pour les poissons d'écloserie. Contrairement à la compréhension actuelle, une grande proportion de la mortalité des saumons du stade du saumoneau à celui d'adulte, communément appelée la « mortalité marine », pourrait en fait se produire avant l'entrée en mer. [Traduit par la Rédaction]

Introduction

Early life-history stages of fishes are thought to be critical periods of high and variable mortality that determine recruitment (Hjort 1914), but the temporal resolution of mortality during earlier stages (i.e., specifically when mortality occurs within a stage) is difficult to quantify compared with later stages. Given myriad natural factors affecting early mortality (Sogard 1997), including those during juvenile migration periods, it is often challenging to detect possible effects of anthropogenic factors or management actions during early stages. Fish hatcheries represent a human influence on a natural system and provide easy access to study juvenile stages, but do not provide natural rearing conditions.

Further, fish reared in hatcheries may diverge genetically from their wild ancestry and otherwise affect native fish fauna. For example, anadromous salmonids released from hatcheries into nearby rivers may interact with wild fish through competition for space or food or through genetic introgression affecting their fitness, which may strengthen over time (Naish et al. 2007). There is great management interest in identifying survival discrepancies between hatchery-reared salmonids and their wild counterparts, but comparisons are most powerful when they occur outside of hatchery-rearing periods, when wild and hatchery-reared fish are faced with the same stressors (i.e., present in the same habitats at the same time) and when hatchery rearing has

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been of short duration, thereby avoiding issues of inbreeding or outbreeding. These conditions, together, are rare for anadromous salmonids.

A train derailed in the Cheakamus River canyon (British Columbia, Canada) on 5 August 2005. From one overturned railway car, 45 000 L of sodium hydroxide (i.e., caustic soda or lye, 73% concentration) was spilled into the river. The highly basic (pH > 9) pulse of NaOH travelled downstream and, before reaching the Squamish River where it was further diluted, killed >90% of free-swimming fish in the mainstem river (McCubbing et al. 2006). Four cohorts of juvenile steelhead trout (*Oncorhynchus mykiss*) were affected (ages 0+ to 3+), with estimated 90% mortality over all age classes (McCubbing et al. 2006). A short-term (2 years) hatchery supplementation program using native brood stock was implemented in an effort to boost adult steelhead returning to the river from 2 of the 3 years of poor forecasted wild smolt production.

Potential management concerns regarding the effectiveness of this hatchery-based restoration effort included lower survival of hatchery-reared smolts (the life-history stage that migrates from fresh water to salt water) during the downstream and ocean migration compared with wild smolts and high levels of freshwater residualization (i.e., failure to migrate; Ricker 1938) of hatchery smolts. Both factors could limit adult returns and therefore produce little benefit at great cost for the program. A literature review showed that between 2% and 9% of hatchery-reared steelhead typically residualize, ranging as high as 17% in some studies (Hausch and Melnychuk 2012). Residualization could be either temporary (with smolts remaining in fresh water an extra year and outmigrating the following year) or permanent (remaining in fresh water until maturity), and hatchery residuals could compete with wild juveniles for space and resources, thereby affecting their growth (McMichael et al. 1997), or directly feed on smaller wild fish.

Several studies have compared survival of migrating salmon smolts between wild and hatchery rearing histories, but results have been equivocal. Some suggested higher survival of wild smolts (Chittenden et al. 2008; Welch et al. 2004), while others showed no consistent differences between rearing histories (Johnson et al. 2010; Lacroix 2008; Moore et al. 2010; Thorstad et al. 2007). Studies that compared wild and hatchery survival during the full smolt-to-adult period (commonly termed “marine survival”, although it typically includes the in-river freshwater migration) have tended to find wild survival advantages, but have also found mixed results (Jokikokko et al. 2006; Kostow 2004; Zabel and Williams 2002). The first few weeks when smolts are actively migrating is arguably the most important period determining recruitment (Percy 1992; Ricker 1976), so comparing survival between wild and hatchery-reared fish during the early migration could provide insight into relative differences of total marine survival and therefore fitness.

To address hypotheses of lower survival during the migration and higher residualization of hatchery-reared steelhead smolts relative to wild smolts, we used acoustic telemetry and mark-recapture methods. Hatchery-reared smolts were tagged and released into the Cheakamus River in 2007 and 2008. In 2006 and 2007, insufficient numbers of wild smolts were available for tagging. The 2007 year therefore provided survival estimates of only hatchery-reared smolts. Previous studies in 2004 and 2005 on wild Cheakamus River steelhead (Melnychuk et al. 2007) produced estimates for only wild smolts. Sufficient wild smolts were caught in 2008, allowing for a direct comparison of survival and residualization between rearing histories in the same year (data from earlier years were included in the analysis to provide greater generality, but results are consistent with an analysis limited to only 2008). Estimated residualization rates were reported previously for wild and hatchery-reared fish separately (Melnychuk 2009b) or combined (Melnychuk and Hausch 2011). This paper compares survival during the downstream and early ocean migration between wild-

origin and hatchery-reared steelhead smolts and also compares smolt-to-adult return rates and smolt travel times between wild and hatchery groups. We hypothesize lower overall survival of hatchery-reared smolts compared with wild smolts and further aim to identify specifically where and when periods of high mortality occur for wild and hatchery groups.

Materials and methods

Study site and stationary receivers

All six salmon species resident of British Columbia (including steelhead) inhabit the Cheakamus River along with other salmonids (*Oncorhynchus* spp. and *Salvelinus* spp.), lampreys (*Lampetra* spp.), sculpins (*Cottus* spp.), and mountain whitefish (*Prosopium williamsoni*) (McCubbing et al. 2006). Many of these species are anadromous and some were at sea at the time of the railway spill, but most species that were present in the river were directly affected, with estimated mortalities of >90% in most age classes (McCubbing et al. 2006). Tenderfoot Creek Hatchery is operated by Fisheries and Oceans Canada, at which several salmon species (but not steelhead prior to the spill) are reared and released as fry or smolts into Tenderfoot Creek, a short distance from the Cheakamus River (Fig. 1).

The Cheakamus River, a fifth-order river regulated by a dam, with a mean annual discharge of 31.5 m³·s⁻¹, drains into the Squamish River before reaching Howe Sound and Georgia Strait (Fig. 1). The total distance from release locations of tagged smolts in the Cheakamus River to the mouth of the Squamish River ranged from 15.9 to 27.5 km. Exit routes to the Pacific Ocean include Queen Charlotte Strait to the north and Juan de Fuca Strait to the south (Fig. 1). Prior to releasing smolts, we installed acoustic receivers (VR-2 or VR-3, VEMCO Ltd., Bedford, Canada) arranged in listening lines in Howe Sound (HS_{inner} and HS_{outer}), the northern Strait of Georgia (NSOG), Queen Charlotte Strait (QCS), and Juan de Fuca Strait (JDF; Fig. 1; details in Melnychuk et al. 2007). We also installed receivers as single or paired units at several locations in Tenderfoot Creek, the Cheakamus River, and the Squamish River (Fig. 1) to monitor movements of tagged fish. River receivers were in place until at least early June in all years (see Fig. A1 in Appendix A).

Fish release groups

Hatchery steelhead smolts were reared from eggs collected from wild Cheakamus River adults. Adults were spawned (spring 2006 and 2007) and eggs were incubated (summer 2006 and 2007) at Fraser Valley Trout Hatchery (FVTH). In September of each year, a portion of the fry was transferred to Tenderfoot Creek Hatchery (TCH). Fry were reared until smoltification the following spring at both hatcheries. Smolts were tagged 8–10 days before release in 2007 and 22–27 days before release in 2008. They were either released into Tenderfoot Creek voluntarily (TCH fish) or transported and released into the Cheakamus River (FVTH fish; Fig. 1). Wild (W) smolts were caught during their downstream migration in side channel traps and rotary screw traps in the Cheakamus River. They were held for up to 21 days (2004), 17 days (2005), or 7 days (2008) in traps until fish could be tagged and were released 1–5 days after tagging near original capture sites (Fig. 1). In 2008, one tag-related mortality and one tag extrusion were observed in wild smolts prior to fish release, but otherwise there were no signs of tag rejection, infection, or altered behaviour in any release group in any year. Acoustic tags that transmitted at 69.0 kHz (V9-6L, VEMCO Ltd., Bedford, Canada) were implanted into smolts using standard surgical procedures (Melnychuk et al. 2007; Welch et al. 2007).

A total of 398 tagged fish were released over 4 years, spread among 11 release groups (Table 1). Release dates ranged from 5 to 24 May. One group (FVTH RG1 in 2008) was released further upstream than others, approximately 15 km upstream of the Cheakamus River and Squamish River confluence (Fig. A2). Another group (FVTH in 2007) was released further downstream than

Fig. 1. Map of study area. Base map shows locations of acoustic receiver lines across inshore straits, thick lines indicated by arrows. Inset maps show Cheakamus and Squamish rivers with locations of single or paired receivers, as circles. Release sites of tagged smolts are shown by a solid "X" for wild groups and by an outlined "X" for hatchery-reared groups, with labels A-E listed in Table 1. For the coloured version of this figure, refer to the Web site at <http://www.nrcresearchpress.com/doi/full/10.1139/cjfas-2013-0165>.

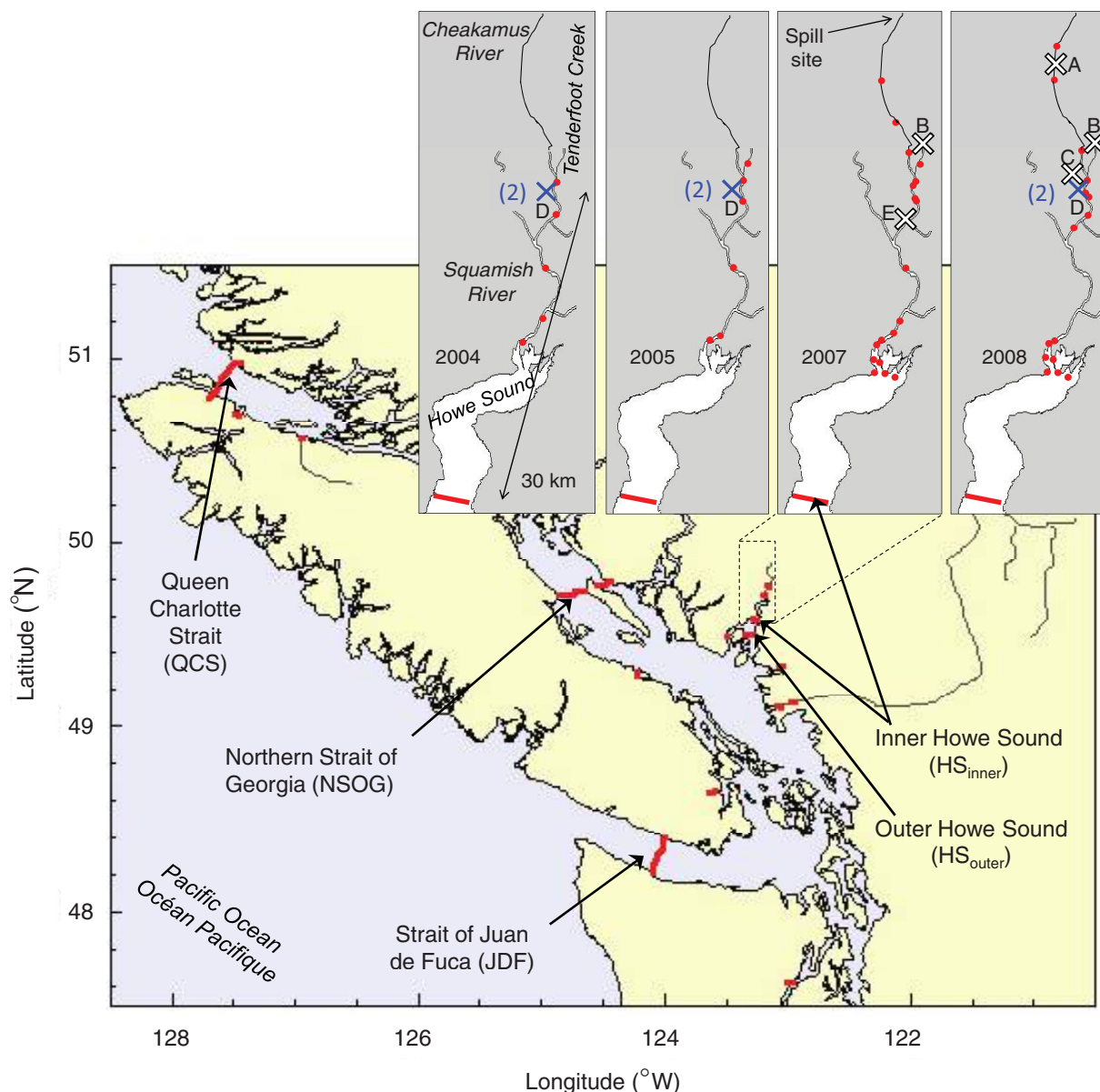


Table 1. Release groups of tagged Cheakamus River steelhead smolts.

Release year	Rearing history	Release group	Release date	Release location on map	Fork length (mm)		
					Mean (SD)	Range	n released
2004	W	1	8 May	D	185.1 (16.8)	148–226	42
2004	W	2	24 May	D	181.3 (20.1)	153–215	9
2005	W	1	6 May	D	177.5 (14.2)	153–212	44
2005	W	2	19 May	D	177.8 (13.4)	160–197	5
2007	H (TCH)	1	6 May	B	186.4 (9.6)	172–206	19
2007	H (FVTH)	1	23 May	E	182.6 (11.6)	163–210	81
2008	W	1	6 May	D	177.6 (12.7)	149–209	72
2008	W	2	12 May	D	178.8 (9.5)	158–203	28
2008	H (TCH)	1	5 May	B	176.7 (8.7)	158–192	40
2008	H (FVTH)	1	8 May	A	183.7 (13.6)	155–206	40
2008	H (FVTH)	2	22 May	C	188.4 (10.0)	167–205	18

Note: W, wild; H, hatchery; TCH, Tenderfoot Creek Hatchery; FVTH, Fraser Valley Trout Hatchery.

others, approximately 3.6 km upstream of the confluence. The remaining nine groups were released within 1.5 km of each other, either at TCH or in a side channel of the Cheakamus River near Tenderfoot Creek (Figs. 1, A2). Mean fork length varied among years and release groups and on average was slightly greater for hatchery-reared groups than for wild groups (Table 1).

Segment distances were measured with mapping software as shortest-route in-water distances between receiver stations. These (Fig. A2) were added for measures of cumulative distance from release to successive stations. Cumulative travel times were measured as the time from release until the first detection of a tag at a station and were averaged across fish within each release group. We calculated 95% confidence intervals (CI) around mean cumulative travel times for each release group.

Mark–recapture analysis for smolt survival estimation

Mark–recapture models based on the Cormack–Jolly–Seber (CJS) model (Cormack 1964; Jolly 1965; Seber 1965) were used to estimate survival probabilities (ϕ) in each segment of the migration and detection probabilities (p) at each river receiver or line of ocean receivers. See Appendix A for mark–recapture assumptions and detailed methods. One particularly important assumption is that fish did not cease their migration prior to encountering receivers or between any stations where they would not be detected (i.e., we assume that freshwater residualization rates were negligible). The potential for residualization is considered elsewhere (Melnychuk and Hausch 2011), and ϕ are interpreted with the caveat that they may be confounded with residualization; we actually estimate “apparent survival”, though unless otherwise specified we use “survival” throughout the manuscript for simplicity.

To compare survival between wild and hatchery-reared fish, we accounted for possible effects of fork length (FL, as an individual covariate), release date (RD, group covariate), and migration distance (d , group- and segment-specific covariate). We also considered possible effects of release group and river level (a measure of water height during the mean arrival time of each release group at each river station) on p . These above factors were included in models directly as covariates affecting $\logit(p)$ or $\logit(\phi)$; candidate models were treated as competing hypotheses and compared using information-theoretic methods (QAIC_c) on the basis of their fit to the data and the number of parameters in the model required to achieve that fit. Release groups from all years were combined in the same analysis to allow the effects of covariates on ϕ or p to be consistent across years and across segments or stations (see Appendix A for details). We used a sequential approach for model comparison, first comparing models for p while keeping constant a general model for ϕ , and then comparing models for ϕ having selected the model for p with the lowest QAIC_c value (e.g., Melnychuk 2009a; Zabel and Achord 2004). Although this approach is considered ad hoc, it limits what could otherwise be a very large number of possible candidate models to a more reasonable number and has been shown to have little effect on bias and precision of parameter estimates (Doherty et al. 2012).

In previous studies, we observed river level (or discharge) to exert a strong influence on p at river receiver stations (Melnychuk 2009a; Welch et al. 2011). Higher river levels and faster flows, typically later in the migration season, result in decreased p because of greater background noise and (or) smolts spending less time within detection range of a receiver as they travel downstream. The 11 groups were released at different times (Table 1) and thus faced different flow conditions in the Cheakamus and Squamish rivers (Fig. A1). We accounted for potential effects of river level on p by constraining p in some models to be functions of the river level experienced by release groups at each receiver station. To quantify the river level covariate, the mean arrival time of each group at each station was calculated, and the corresponding river level at the mean arrival time was used as a group-specific covariate. Detection probabilities at ocean receivers were

modelled as common across release groups within a given year. Detection probabilities were estimated for the two Howe Sound stations and the NSOG station. They could not be estimated for the (pooled) terminal detection station at QCS–JDF, however, as there were no detection data further along migration routes to inform detection probabilities at this terminal station. Instead, we assumed fixed values for $p_{\text{QCS–JDF}}$ based on year-specific estimates of p_{NSOG} with slight adjustment for receiver coverage on each line (Melnychuk 2009b; Appendix A), which allowed survival probabilities in the terminal segment to be estimable.

We hypothesized nine models for survival. One was the general CJS model, with separate parameters estimated for each segment for each release group and no effect of fork length or release date. The remaining eight models allowed for additive effects of fork length and release date on $\logit(\phi)$, as these were observed to be important influences in previous studies (Bilton et al. 1982; Melnychuk 2009b; Sogard 1997; Welch et al. 2009). Four models assumed independence among segments and years (i.e., separate survival parameters were estimated for each segment in each year, but these parameters were common across release groups within a given year). The other four models assumed that mortality is proportional to distance travelled, with $\logit(\phi_{\text{seg}})$ constrained to be a linear function of segment length. We allowed for separate survival–distance relationships in the Cheakamus River, the Squamish River, and coastal waters. For the four segment:year models and the four distance-based models, we considered influences of (i) an additive covariate of wild or hatchery-rearing on $\logit(\phi)$; (ii) initial mortality parameters $M_{\text{initial,W}}$ and $M_{\text{initial,H}}$ which provide flexibility in ϕ in the first segment after release regardless of where that segment occurs in relation to migration routes of other release groups (details in Appendix A); (iii) both of these wild or hatchery mortality effects; and (iv) neither effect. See Appendix A for detailed model descriptions.

Wild and hatchery-reared adult returns and smolt-to-adult survival

Anadromous salmonids display homing behaviour and typically return to natal rivers to spawn after several years at sea. Hatchery-reared smolts from the two hatcheries had their adipose fins clipped, which allow returning adults that reared in hatcheries to be distinguished from those of wild origin. Steelhead have a flexible timing of smoltification and spawning, so freshwater and marine age structures are variable; wild Cheakamus River steelhead typically smolt at age 2 or 3, while hatchery-reared fish smolt after the first year. Cheakamus River steelhead typically spend 2 or 3 years at sea, so fish that were released in 2007 and 2008 returned in 2009, 2010, or 2011. Snorkel surveys and angler surveys in 2009–2011 were used to estimate the number of wild and hatchery-reared adults returning to the Cheakamus River (Korman et al. 2012).

Cheakamus River steelhead have a winter-run life history, returning to fresh water between late fall and early spring. Given the typical summer timing of commercial salmon fisheries, they are not vulnerable to commercial fishing. All recreational angling is catch-and-release, though there may be some native harvest of unknown quantity. We assume that catch of adult steelhead is negligible, so total marine survival can be calculated separately for wild and hatchery-reared fish as the number of returning adults divided by the number of outmigrating smolts. The number of wild smolts in 2007 could not be estimated. The number of wild smolts in 2008 was estimated to be $13\,894 \pm 5063$ SD (Schwarz and Bonner 2012). The total number of hatchery-reared smolts released in 2008 was 17 618.

Survival estimates from mark–recapture models are “apparent survival” because possibilities of mortality and permanent residency between receiver stations cannot be distinguished from detection data. The most likely cause of permanent residency is due to freshwater residualization, or the cessation of active migration

after release in fresh water. Estimates of the proportion of wild (R_W) and hatchery (R_H) fish residualizing in the Cheakamus River (Melnychuk 2009b) were used to adjust apparent survival estimates ($\hat{\phi}_W, \hat{\phi}_H$) to better represent actual survival estimates ($\hat{\phi}'_W, \hat{\phi}'_H$) during the smolt migration:

$$(1) \quad \hat{\phi}'_W = \frac{\hat{\phi}_W}{1 - R_W}$$

$$\hat{\phi}'_H = \frac{\hat{\phi}_H}{1 - R_H}$$

Residualization is assumed to occur in the first segment of the migration after release and therefore affects all estimates of survivorship from release to successive detection stations.

Results

Steelhead migration patterns

Tagged smolts generally moved downstream immediately after release (Fig. 2). Travel speeds were especially rapid for wild fish. Fish that survived to the mouth of the Squamish River were detected on average 1.9 days after release for W RG2 in 2004 (95% CI, 0.54–3.21 days) and 21.4 days after release for TCH in 2008 (95% CI, 12.6–30.2 days); other groups were within this range. Some hatchery groups averaged more than 1 week to travel from river mouth to inner Howe Sound line, while other hatchery groups and all wild groups took only a few days; the variation around mean travel times was also generally less for wild groups (Fig. 2). Slower travel speeds of hatchery fish continued through Howe Sound to the NSOG line, with mean cumulative travel times of 8–20 days for wild groups (overall mean, 15.3 days; range of lower 95% CI, 6.5–17.3 days; range of upper 95% CI, 10.4–23.3 days) and 23–47 days for hatchery groups (overall mean, 33.5 days; range of lower 95% CI, 9.7–34.3 days; range of upper 95% CI, 36.1–58.8 days). There were few detections of hatchery-reared fish on the outer lines at QCS and JDF.

Detection probabilities

Estimated detection probabilities varied widely across receiver stations, typically around 0.5–0.8 for river stations and 0.7–0.9 for ocean stations (Appendix A, Fig. A3). The comparison of p models while keeping constant a general ϕ model resulted in strong support for the model with separate river level covariates for Cheakamus River and Squamish River stations ($\phi(\text{seg};G)$, $p(S;Y + \text{lev}_{\text{Chk}} + \text{lev}_{\text{Sqm}})$; Table 2). Despite involving only a single extra parameter for the Squamish River covariate, the negative log-likelihood of the model was much lower (i.e., the model fit the data considerably better) than the model $\phi(\text{seg};G)$, $p(S;Y + \text{lev}_{\text{Chk}})$, which had a corresponding ΔQAIC_c of 14.8. For both rivers, p decreased as river level increased. Models for p that use environmental covariates are also preferred as they are less likely to contain inestimable parameters and less likely to have some parameter estimates sensitive to limited detection data of some release groups at some receiver stations (see Appendix A). The general CJS model required estimating more parameters and was less parsimonious, with ΔQAIC_c of 6.8.

Survival during the smolt migration

There was a strong overall effect of wild or hatchery-rearing history on survival. The QAIC_c -preferred model for ϕ was $\phi(d_{\text{Chk}} + d_{\text{Sqm}} + d_{\text{sw}} + \text{FL} + \text{RD} + \text{HW} + M_{\text{initial,H}} + M_{\text{initial,W}})$, $p(S;Y + \text{lev}_{\text{Chk}} + \text{lev}_{\text{Sqm}})$ (Table 3). Under this model, wild smolts had greater overall survival than hatchery smolts across monitored segments of the migration ($\beta_W = 0.91$ relative to the hatchery (H) reference group, 95% CI, 0.49 to 1.34). Wild smolts also showed some evidence of greater initial survival in the first segment after release ($\beta_{M_{\text{initial,W}}} = -0.71$, 95% CI, -1.58 to 0.16) than hatchery-reared smolts

Fig. 2. Travel times of release groups in (a) 2004, 2005, and 2007 and (b) 2008 past detection stations up to the inner Howe Sound line. Data points show cumulative travel time estimates since release plotted against cumulative distance travelled. For each release group, the last data point corresponds to HS_{inner}; the second-to-last data point, 11–13 km before this, represents the furthest downstream detection station in the Squamish River. Wild groups (W) are shown by circles–squares–diamonds, while hatchery groups (Tenderfoot Creek Hatchery, TCH; Fraser Valley Trout Hatchery, FVTH) are shown by triangles. RG1 and RG2 denote first and second release groups, respectively, within the same year. Error bars show 1 SE. Travel time estimates for the wild release groups in 2004 and 2005 in panel (a) were previously shown in Melnychuk et al. (2007). For the coloured version of this figure, refer to the Web site at <http://www.nrcresearchpress.com/doi/full/10.1139/cjfas-2013-0165>.

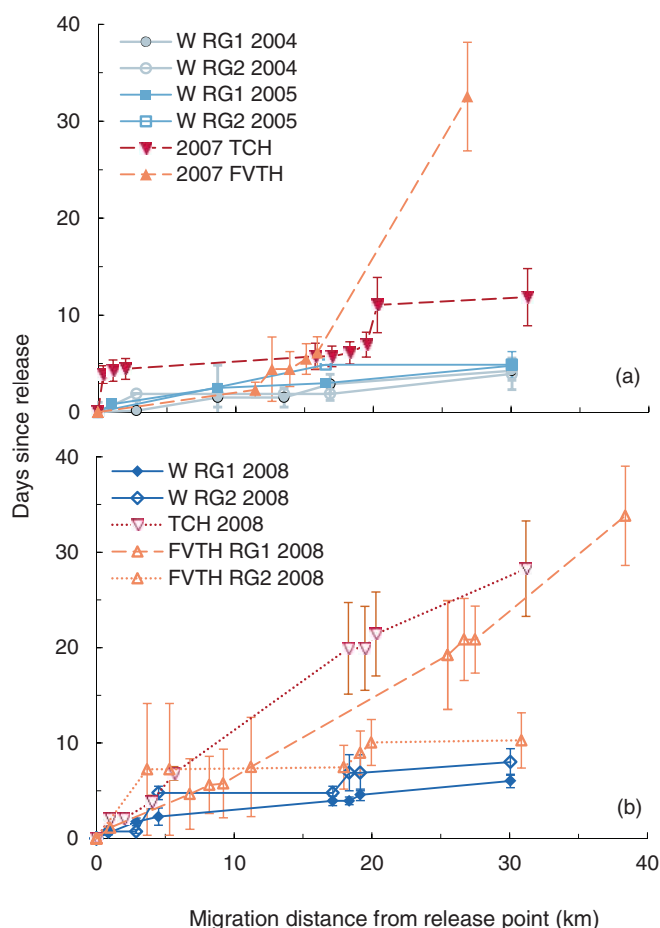


Table 2. Model selection results for detection probability (p) submodels.

Model	k	$-2\ln(L)$	QAIC_c	ΔQAIC_c
$\phi(\text{seg};G)$, $p(S;Y + \text{lev}_{\text{Chk}} + \text{lev}_{\text{Sqm}})^*$	149	2794.3	2512.2	0.0
$\phi(\text{seg};G)$, $p(S;G)$	201	2636.8	2519.0	6.8
$\phi(\text{seg};G)$, $p(S;Y + \text{lev}_{\text{Chk}})^*$	148	2816.3	2527.0	14.8
$\phi(\text{seg};G)$, $p(S;Y)^*$	147	2867.8	2564.8	52.6

Note: Quantities shown are number of parameters (k), log-likelihoods and QAIC_c values (adjusted for small sample sizes and extrabinomial variation with $\hat{c} = 1.279$). Submodels for p are compared while the fully time- (seg) and group-varying CJS submodel for ϕ is held constant ($\phi(\text{seg};G)$). The final station p is fixed according to year-specific predictions ranging from 0.855 to 0.923 (Appendix A). S, station; seg, segment; G, release group; Y, year (group covariate); lev_{Chk} and lev_{Sqm} , river levels in the Cheakamus River or Squamish River, respectively, at the mean arrival time of a particular release group at a particular station (group- and station-specific covariate). See Appendix A for detailed model descriptions.

*Models contain four group-specific p parameters for the NSOG station, for groups that showed split-route migration patterns beyond Howe Sound (Appendix A).

Table 3. Model selection results for survival (ϕ) submodels.

Model	k	-2ln(L)	QAIC _c	ΔQAIC _c
$\phi(d_{\text{Chk}} + d_{\text{Sqm}} + d_{\text{sw}} + \text{FL} + \text{RD} + \text{HW} + M_{\text{initial,H}} + M_{\text{initial,W}})$	52	2928.2	2396.9	0.0
$\phi(d_{\text{Chk}} + d_{\text{Sqm}} + d_{\text{sw}} + \text{FL} + \text{RD} + M_{\text{initial,H}} + M_{\text{initial,W}})$	51	2951.9	2413.2	16.4
$\phi(\text{seg:Y} + \text{FL} + \text{RD} + \text{HW} + M_{\text{initial,H}} + M_{\text{initial,W}})$	89	2849.5	2416.0	19.2
$\phi(d_{\text{Chk}} + d_{\text{Sqm}} + d_{\text{sw}} + \text{FL} + \text{RD} + \text{HW})$	50	2958.3	2416.1	19.3
$\phi(\text{seg:Y} + \text{FL} + \text{RD} + \text{HW})$	87	2856.6	2417.1	20.3
$\phi(\text{seg:Y} + \text{FL} + \text{RD} + M_{\text{initial,H}} + M_{\text{initial,W}})$	88	2859.8	2421.9	25.0
$\phi(\text{seg:Y} + \text{FL} + \text{RD})$	86	2870.7	2425.9	29.1
$\phi(d_{\text{Chk}} + d_{\text{Sqm}} + d_{\text{sw}} + \text{FL} + \text{RD})$	49	3010.9	2455.1	58.3
$\phi(\text{seg:G})$	149	2794.3	2512.2	115.4

Note: See Table 2 footnotes and Appendix A. Submodels for ϕ are compared while the submodel for p is held constant: $p(\text{S:Y} + \text{lev}_{\text{Chk}} + \text{lev}_{\text{Sqm}})$. FL, fork length (individual covariate); RD, release date (group covariate); HW, rearing history (hatchery or wild, respectively; group covariate); $M_{\text{initial,H}}$ and $M_{\text{initial,W}}$, initial mortality in the first segment after release, common across all hatchery groups or wild groups (respectively), and additive on the logit scale to the baseline mortality within each segment (group covariate); d_{Chk} , d_{Sqm} , and d_{sw} , per-unit distance mortality constraints with separate slopes for Cheakamus River, Squamish River, and salt water, respectively (group- and segment-specific covariate).

($\beta_{M_{\text{initial,H}}} = -1.40$, 95% CI, -1.93 to -0.88). There was essentially no support for other survival models (Table 3). In general, models with only one type of hatchery or wild effect (HW, or $M_{\text{initial,W}}$ and $M_{\text{initial,H}}$) performed poorer than the model with both types, and the model with neither type performed poorer still. Distance-based models required 37 fewer parameters to be estimated than their counterparts with segments and years estimated independently and generally performed better. The general CJS model had parameters for some release groups that were estimated at boundaries (Appendix A, Figs. A3, A5) and performed the poorest of all models (Table 3).

There was a strong positive effect of fork length on survival ($\beta_{\text{FL}} = 0.020$, 95% CI, 0.007 to 0.032). There was a weak effect of release date on survival, with slightly lower survival associated with later releases ($\beta_{\text{RD}} = -0.018$, 95% CI, -0.043 to 0.007). The reduction in survival with increasing distance travelled was greatest in the Cheakamus River ($\beta_{d_{\text{Chk}}} = -0.23$, 95% CI, -0.43 to -0.03), intermediate in the Squamish River ($\beta_{d_{\text{Sqm}}} = -0.08$, 95% CI, -0.13 to -0.02), and least in ocean segments ($\beta_{d_{\text{sw}}} = -0.014$, 95% CI, -0.017 to -0.011). A comparison of relative effect size on survival of the covariates contained in the top model from Table 3 is given in Fig. A4, showing the strong influences of wild versus hatchery rearing across all segments and initial mortality of hatchery smolts in the first segment after release.

Survivorship declines predicted by the top model from Table 3 are shown in Fig. 3, plotted against minimum cumulative distance travelled. Survivorship estimates (i.e., the product of segment-specific $\hat{\phi}$) from release to river mouth were 69%–82% for wild groups and 23%–36% for hatchery-reared groups (Fig. 3a; Table A1). The same estimates plotted on a log scale (Fig. 3b) allow for comparisons of mortality rates per distance travelled, represented by the slopes for a given segment. The steepest declines in survivorship were in the first segment, especially for hatchery groups (Fig. 3b). After ocean entry, differences in survivorship declines in the Howe Sound segments and to NSOG were less pronounced between wild and hatchery-reared fish. The discrepancy at exit from the Georgia Strait system via QCS or JDF was large, with estimated survivorship of wild groups at 21%–33% and that of hatchery-reared groups at 3.2%–6.1% (Fig. 3a; Table A1).

Wild and hatchery-reared adult returns and smolt-to-adult survival

From the 2008 cohorts of wild and hatchery Cheakamus River steelhead outmigrants, an estimated 1114 wild adults and 723 hatchery-reared adults returned between 2009 and 2011 (Korman et al. 2012). Assuming negligible catch of adult steelhead, total marine survival rate estimates are $1114/13\ 894 = 8.0\%$ for wild smolts and $723/17\ 618 = 4.1\%$ for hatchery-reared smolts. The wild return rate estimates are especially uncertain owing to the large standard deviation in the estimated number of smolts in 2008

($13\ 894 \pm 5063$ SD; Schwarz and Bonner 2012), but we can quantify the effects of this uncertainty by performing the calculation using a higher or lower number of smolts in the denominator instead of the mean estimate. If instead we assume more wild smolts (+1 SD, or +2 SD) or fewer wild smolts (-1 SD, or -2 SD) in the denominator, we calculate return rates of 5.9%, 4.6%, 12.6%, or 29.6%, respectively, which are all still above the estimated return rate of hatchery smolts (4.1%).

Recall that mark-recapture survival estimates $\hat{\phi}$ reported above are actually “apparent survival”, as they do not account for the possibility of live smolts stopping their migration between receiver stations. If estimates of freshwater residualization (2.1% for wild smolts and 8.8% for hatchery smolts; Melnychuk 2009b) are used to adjust apparent survival estimates (Table A1) to better estimate actual survival ($\hat{\phi}'$, eq. 1), adjusted survivorship estimates from release to the river mouth are 71%–84% (wild) and 26%–40% (hatchery) and from release to exit from the Strait of Georgia are 22%–33% (wild) and 3.5%–6.7% (hatchery). Taking the ratio of mean adjusted survivorship estimates, the survival advantage of wild smolts compared with hatchery smolts was 2.3-fold after the downstream migration, similar to the 2.0-fold estimated for total marine survival. That is, similar magnitudes of the survival discrepancy between wild and hatchery-reared fish occurred by the end of the freshwater migration and the return of adult spawners.

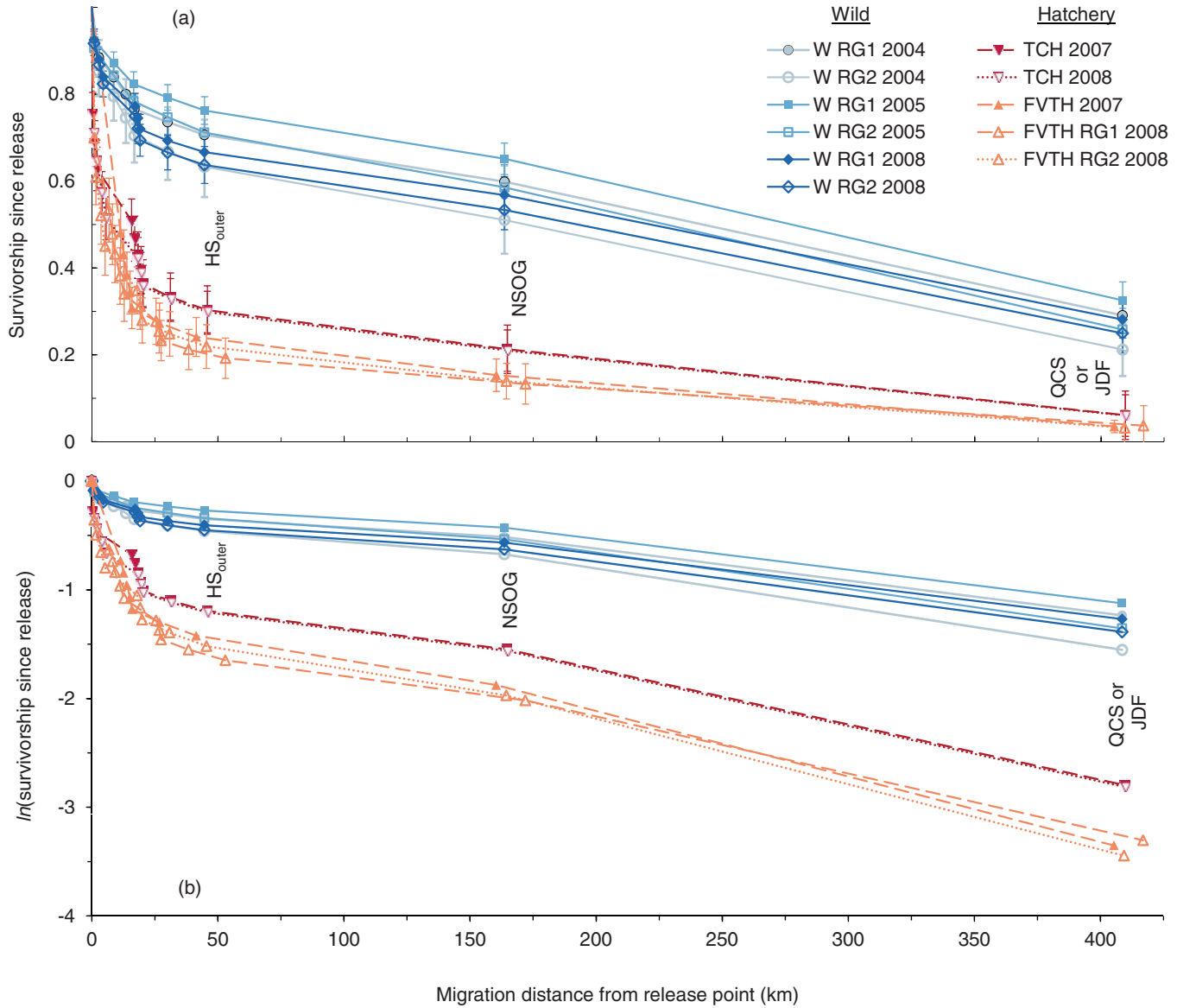
Discussion

In this study, we addressed a key concern about a management program implemented in response to the adverse ecological impacts from a chemical spill; survival of hatchery-reared smolts would be poorer than wild smolts, limiting the number of adult spawners returning to the river during a critical period of reduced abundance. We detected a wild survival advantage over hatchery fish throughout the monitored migration, with a large discrepancy established immediately after release, in fresh water. The estimated difference in freshwater residualization between wild and hatchery smolts does not appear to be great enough to explain the observed survival difference early in the downstream migration. This early survival difference was similar to the estimated difference at the time of adult returns.

Survival differences between wild and hatchery-reared smolts

Despite similar brood stock origins, survival during the smolt migration was clearly higher for wild smolts than hatchery-reared smolts. This difference was consistent across assumptions of mark-recapture model structures as well as with an analysis limited to 2008, the only year in which both wild and hatchery smolts were released (Melnychuk 2009b). Estimated survival after release of hatchery smolts or after enumeration of wild smolts is commonly

Fig. 3. Survivorship estimates from release to successive detection stations during the smolt migration on (a) a linear scale and (b) a natural logarithmic scale, prior to adjustment for residualization. Estimates are shown assuming model $\phi(d_{\text{Chk}} + d_{\text{Sqm}} + d_{\text{sw}} + \text{FL} + \text{RD} + \text{HW} + M_{\text{initial,H}} + M_{\text{initial,W}})$, $p(S;Y + \text{lev}_{\text{Chk}} + \text{lev}_{\text{Sqm}})$, plotted against minimum migration distance from release location. Wild groups (W) are shown by circles–squares–diamonds, while hatchery groups (Tenderfoot Creek Hatchery, TCH; Fraser Valley Trout Hatchery, FVTH) are shown by triangles. Error bars in panel (a) show 1 SE. For the coloured version of this figure, refer to the Web site at <http://www.nrcresearchpress.com/doi/full/10.1139/cjfas-2013-0165>.



termed “marine survival”, although a large proportion of the total mortality occurring during this “marine” life-history period actually occurred before leaving fresh water; approximately 60%–74% of hatchery smolts and 16%–29% of wild smolts died before ocean entry. If we had enumerated fish at only the endpoints of the smolt-to-adult period as is commonly done, we would have concluded there were wild and hatchery differences in “marine survival” and reasoned that this difference was likely established sometime during the 2–3 years of ocean life, since the freshwater migration period is so brief. The high resolution of acoustic receivers in rivers (Figs. 1, A2), however, allowed us to observe that these “marine survival” differences were actually established earlier, largely prior to ocean entry.

Previous studies have compared survival between wild and hatchery-reared salmonids, both during the smolt migration and for the smolt-to-adult period. Studies from two British Columbia

watersheds showed higher proportions of wild fish than hatchery fish detected at ocean acoustic receivers, implying higher survival of wild steelhead smolts (Welch et al. 2004) and coho salmon (*Oncorhynchus kisutch*) smolts (Chittenden et al. 2008) during the migration. In contrast, no survival differences were detected between wild and hatchery-reared steelhead smolts in the downstream and estuarine migrations from coastal rivers in Washington (Moore et al. 2010) or Oregon (Johnson et al. 2010). Steelhead smolts from other coastal rivers in Washington showed mixed results (Moore et al. 2012). Atlantic salmon (*Salmo salar*) also showed either no difference during the smolt migration (Thorstad et al. 2007) or higher survival in wild smolts during an earlier (estuarine) portion of the migration but not during a later (coastal inshore) portion (Lacroix 2008).

More commonly, studies have compared survival over the full smolt-to-adult period. In all the following examples, tagged wild

and hatchery smolts were released in fresh water so survival estimates implicitly incorporated at least some portion of the downstream migration, similar to our study. Wild steelhead smolts from the Hood River, Oregon, had sevenfold higher smolt-to-adult survival than smolts from a newly implemented hatchery program, which, similar to our study, used wild brood stock for eggs (6.1% and 0.9% survival, respectively; Kostow 2004). Total marine survival was consistently higher for wild steelhead than for hatchery-reared smolts from the Columbia River basin (Raymond 1988; Reisenbichler and Rubin 1999). Recapture rates of Atlantic salmon tagged as smolts and caught as adults in fishing gear were two to three times higher for wild fish than hatchery-reared fish in the Baltic Sea (Jokikokko et al. 2006). Finally, in Chinook salmon (*Oncorhynchus tshawytscha*) from the Columbia River basin (Zabel and Williams 2002) and from New Zealand (Unwin 1997), survival of wild smolts was higher than that of hatchery-reared smolts of the same size, but the larger body size of hatchery smolts compensated for this, so return rates of hatchery fish were higher. In our study, hatchery fish were slightly larger on average than wild fish, but size differences were accounted for when estimating survival.

The most likely explanation for the lower observed survival of hatchery-reared fish during the downstream migration is a higher vulnerability to predation (reviewed in Mesa et al. 1994 and Olla et al. 1998) owing to their protection from natural selection prior to hatchery release. Wild steelhead are subjected to predation and environmental stressors for 2–3 years prior to smoltification, resulting in a more-fit subset of the population remaining at the time of tagging. In contrast, hatchery-reared fish are not exposed to such pressures, so a higher proportion of less-fit individuals was likely tagged. The greater initial mortality component of hatchery-reared fish in the first segment of the migration supports the assertion that less-fit individuals are more likely to die soon after release.¹ However, we cannot distinguish from our study what proportion of the extra mortality observed in hatchery-reared smolts has a genetic or disease component and what proportion is simply a learned response to predators. Possible mechanisms of higher mortality in hatchery fish include increased predation risk from feeding at the surface more often (Vincent 1960), having lighter skin coloration (Donnelly and Whoriskey 1991), or having reduced escape responses (Woodward and Strange 1987). Adult bull trout (*Salvelinus confluentus*) are common in the Cheakamus River (Ladell et al. 2010; Melnychuk 2009b). Merganser ducks (*Mergus merganser*) aggregate and feed on outmigrating salmonid smolts (Wood 1987) and are commonly observed on the Cheakamus River. Harbour seals (*Phoca vitulina*) are also seen as far upstream as the confluence of the Cheakamus and Squamish rivers and are a well-known predator of salmon smolts (Greenstreet et al. 1993; Laake et al. 2002). Higher avian predation rates on hatchery smolts than on wild smolts have been observed in other salmonids soon after release (Dieperink et al. 2001), as “naïve” hatchery smolts are particularly vulnerable. Other commonly hypothesized adverse effects of hatchery rearing on fitness, such as inbreeding depression and domestication selection (reviewed in Naish et al. 2007), are less likely to have affected smolts because the hatchery rearing program was of short duration and based on wild brood stock (but see Kostow (2004), in which a large survival decrease was observed in one generation).

Differences in release date do not appear to be a likely explanation for survival differences between wild and hatchery-reared smolts. The weak negative correlation between release date and survival is somewhat consistent with results for coho salmon

(Bilton et al. 1982), where the observed relationship was actually dome-shaped. If hatchery fish smolted and were then released later than physiologically optimal, survival could conceivably be reduced. However, TCH smolts were volitionally released and their survival was comparable to FVTH smolts that were transported and released directly into the river (Fig. 3). Overall, the effect of rearing history on survival was much stronger than a possible release date effect.

Potential confounding of survival with residualization and terminal detection probabilities

We now turn to the assumption that fish did not cease their migration prior to encountering any receivers or between any receiver stations, where they would not be detected. If fish are not detected at a station during their migration, but p at the station is reasonably high (as estimated from other fish detected at and after that station), the most likely explanation under the assumption of no residualization is that fish died prior to arriving at the station. Mark-recapture ϕ are thus “apparent survival”, which are joint probabilities of migration and survival to the station. If some fish from a release group did not migrate consistently but instead residualized in fresh water, survivorship (Fig. 3) would be underestimated for the group. Likewise, localized residualization near the release site could confound estimates of initial mortality represented by parameters $M_{\text{initial,H}}$ and $M_{\text{initial,W}}$, and observed differences in these parameter estimates could reflect differences in residualization along with or instead of differences in initial mortality between wild and hatchery-reared groups. It is possible the minimum-QAIC_c model included these initial mortality parameters because of residualization differences rather than initial mortality differences, but the magnitude of initial mortality differences appears to be much greater than that of residualization differences.

Variation in the extent and timing of migration within salmonid populations is common (Jonsson and Jonsson 1993), resulting mainly from trade-offs of growth potential and survival in different habitats. In this study, residualization differences between wild and hatchery-reared smolts do not appear to be a sufficient explanation for the large apparent survival differences observed. An estimated 2.1% (95% CI, 1.4%–3.9%) of wild smolts and 8.8% (95% CI, 5.3%–20.0%) of hatchery smolts residualized in the Cheakamus River in 2008 (Melnychuk 2009b). This latter estimate is within the range of residualization rates of hatchery-reared steelhead from other watersheds (which averages about 6%; Hausch and Melnychuk 2012). Differences in residualization between wild and hatchery-reared smolts were therefore likely not great enough to account for observed initial mortality differences between wild and hatchery-reared smolts.

Accounting for estimated residualization rates to adjust estimates of apparent survival, the calculated 2.3-fold survival advantage established by ocean entry was similar to the estimated 2.0-fold advantage of wild smolts at the time of adult returns 2–3 years later. To note, the estimated wild/hatchery survival ratio at an intermediate time — exit from the Strait of Georgia — was much higher at 5.6. Possible reasons for this high ratio include differential levels of residency within the Strait of Georgia prior to or instead of leaving for offshore waters, as well as different magnitudes or timing of tag or tagging-related mortality between wild and hatchery smolts, with greater tag-related mortality effects in hatchery fish between ocean entry and exit from the Strait of Georgia system. These possibilities could be addressed in future comparative tagging studies.

We emphasize the comparison of smolt-to-adult survival to mark-recapture survivorship estimates at ocean entry rather

¹Fitness is a lifetime reproductive measure, but if later ocean survival and fecundity are similar between wild and hatchery-reared fish, smolt survival is a reasonable correlate. Others have described this fitness correlate over a short portion of a lifespan as “vitality” (Anderson 2000).

than survivorship estimates at exit from the Strait of Georgia because earlier-station estimates of survival and detection probabilities are often more precise and more accurate than later-station parameter estimates. Detection data from all ocean receiver stations inform detection and therefore survival probabilities for the river mouth station, but there are fewer detection data at final detection stations on which to base survival estimates. These estimates are therefore sensitive to the relatively small number of fish detected at later stations compared with earlier stations. Further, to make survival inferences for the segment leading to the final detection station, we had to assume fixed values of detection probability, as described in Appendix A (based on extrapolations from other ocean stations). This is not expected to bias the relative difference in survival between wild and hatchery groups, but it could bias the overall magnitude of survival estimates in the final segment from NSOG to QCS–JDF, influencing implied survival estimates for the remainder of ocean life as well.

Management implications

The 2-year hatchery rearing program for Cheakamus River steelhead was an attempt to mitigate the impacts of the railway spill by boosting the population of adult spawners in the 2 years (2009, 2010) that would be most affected. Even though survival of hatchery-reared smolts was lower than their wild counterparts, the large number released resulted in a large number of hatchery-reared spawners (Korman et al. 2012). If future conservation-oriented hatchery supplementation programs are implemented and target a certain number of spawners, the number of fish released must compensate for their lower expected survival as well as residualization.

We observed the critical period of differential survival between wild and hatchery-reared fish to be immediately after release, in fresh water. If the discrepancy is entirely a result of hatchery fish being naïve to predation risk and bound to die “if not now, then later”, their lower survival may be inevitable from a management perspective. Conversely, if survival of hatchery-reared fish can be increased during this brief sensitive period, the improvement may persist through adult life. Improved survival of hatchery fish may be realized by varying body size and date of release to determine population-specific optima (Bilton et al. 1982), by restricting fish releases to nighttime hours during which mortality is lower (M. Melnychuk, unpublished data), and by tailoring release times to avoid seasonal periods of predator aggregations (Mace 1983; Wood 1987). Other release strategies can be used to help reduce the frequency of residualization (Hausch and Melnychuk 2012) and to reduce potential impacts on wild populations (Naish et al. 2007).

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Appendix A. Detailed mark–recapture methods and results

Mark–recapture model construction

During their migration, tagged smolts passed a maximum of 7–13 detection stations dependent on year and release group (Fig. 1). Different receiver stations were used in different years, and Fig. A2 summarizes these differences in relation to the release locations of smolt groups. In 2004 and 2005, wild smolts passed one station in the Cheakamus River downstream of the release site and two to three stations in the Squamish River. In 2007, hatchery fish passed zero (FVTH) or three (TCH) stations in the Cheakamus River and five stations in the Squamish River. In 2008, smolts passed a maximum of three to six stations in the Cheakamus River and three stations in the Squamish River. In all years, surviving smolts passed two receiver lines in Howe Sound and one (JDF) or two (NSOG and QCS) receiver lines covering the southern and northern exit routes, respectively (Fig. 1, Fig. A2).

A detection history of an individual fish is a sequence of ones and zeros representing whether the fish was detected or not, respectively, at successive receiver stations during the migration. Detections from the terminal lines at QCS and JDF were pooled to represent exit from the Georgia Strait system. The terminal detection probability $p_{\text{QCS-JDF}}$ was fixed at year-specific values for V9 tags based on year-specific p_{NSOG} estimates, with slight adjustment for receiver coverage on each line (Melnichuk 2009b). After fixing these values, we used the 14-digit individual detection histories in models based on the Cormack–Jolly–Seber (CJS) model (Cormack 1964; Jolly 1965; Seber 1965). The digit before the first detection station encountered represents release, and smolts passing fewer than 13 detection stations had a "0" inserted an appropriate number of times in the detection history before the first "1" representing release.

Mark–recapture models were implemented with Program MARK (White and Burnham 1999; version 7) through RMark (Laake and Rexstad 2009; version 2.1.3). The goodness-of-fit of the general CJS model to detection data was assessed using Program RELEASE (Burnham et al. 1987). We estimated an overdispersion parameter, c (Burnham et al. 1987), using the deviance bootstrap simulation method in Program MARK. We used the estimated value \hat{c} to adjust AIC_c (Akaike's information criterion) values to $QAIC_c$ to guard against selecting overly complex candidate models (Lebreton et al. 1992) and to expand confidence limits on $\hat{\phi}$ and \hat{p} parameter estimates (Burnham et al. 1987).

Detection probability submodels

As detection probability (p) was observed to be influenced by river level or discharge in previous studies, measured river level was used as a covariate of p in three p models. This was especially important given that the 11 release groups were released at various times during the month of May each year (Table 1; Fig. A1) and therefore experienced different river levels during their migrations down the Cheakamus and Squamish rivers (Fig. A1). At each river station, the mean arrival time of each group was calculated and the corresponding river level at that mean arrival time was used as a group-specific covariate. Separate covariates were used for Cheakamus River and Squamish River stations, as a one-unit increase in river level does not necessarily translate into the same decrease in p in both rivers.

Across comparisons of p models, the ϕ model held constant contained interactions between release groups (G) and segments of the migration ($\phi(\text{seg};G)$), allowing independence among groups. This implies that survival can vary not only from overall effects of groups and segments, but from particular combinations of groups and segments. Four p submodels were considered:

1. $p(S;G)$: fully independent p for each group in each year at each station

2. $p(S:Y)$: p common across groups in each year at each station; station and year combinations are independent
3. $p(S:Y + \text{lev}_{\text{Chk}})$: p constrained by an additive effect (on the logit scale) of river level (Cheakamus River only) at the mean arrival time of a group at a station; station and year combinations are independent
4. $p(S:Y + \text{lev}_{\text{Chk}} + \text{lev}_{\text{Sqm}})$: p constrained by additive effects (on the logit scale) of river level (separate effects for Cheakamus River and Squamish River) at the mean arrival time of a group at a station; station and year combinations are independent

This notation implies typical generalized linear model formulation; $\text{logit}(p)$ is modelled as a function of an overall intercept term and coefficient terms multiplied by either values of numerical covariates or levels of categorical covariates. We selected one p model on the basis of QAIC_c scores and used this for comparing ϕ models.

Apart from AIC scores, there are reasons for preferring p models that use environmental covariates. Not all parameters of the general CJS model could be estimated for some groups that had small sample sizes (Table 1), especially at later stations during the migration route. In contrast, more constrained models borrow information from other groups to estimate common parameters (e.g., Lebreton et al. 1992; Melnychuk 2009a). Some parameters under the general CJS model are poorly estimated for two groups because of sparse detection data at some receiver stations. Additionally, owing to random chance, parameter estimates are generally sensitive to the limited amount of detection data at each station when release groups are analyzed separately, so the \hat{p} at a given station vary considerably among groups (even at ocean stations where little variation is expected) and confidence intervals are wide (e.g., for 2008, Fig. A3a). In contrast, the environmental covariate models constrain p to be equal among release groups within a particular year, aside from differences in p among groups because of river level differences at group-specific migration times (Fig. A3b). This seems reasonable since all groups used V9 tags and should therefore have similar probabilities of detection as they migrate past a particular receiver station.

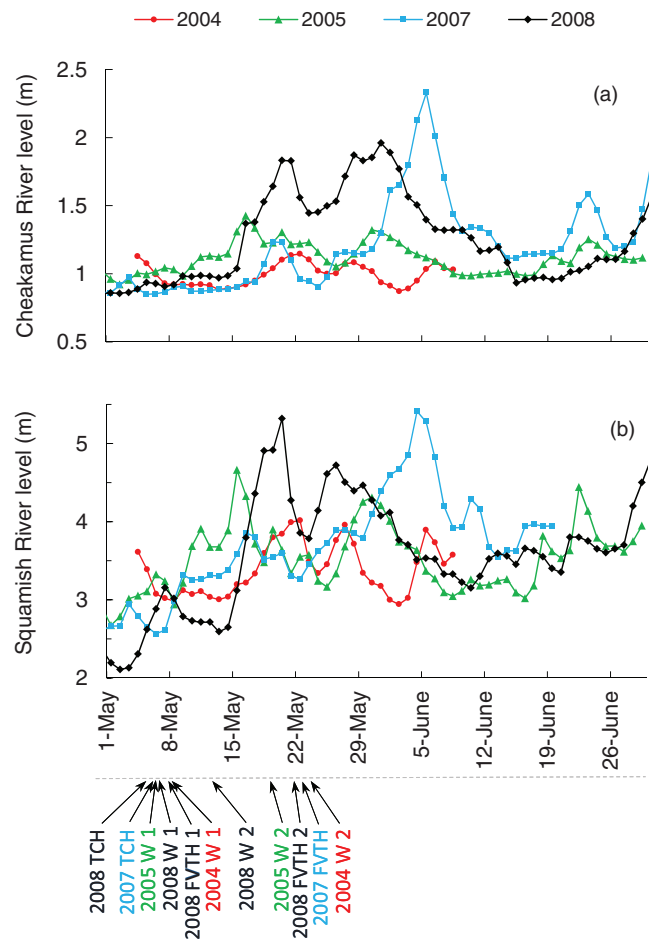
Fish from 6 of the 11 release groups showed evidence of split-route migration patterns, with some fish moving north across QCS and others moving south across JDF. To remove the bias associated with collapsing these split forks into a CJS analysis, four extra p_{NSOG} parameters were incorporated to allow for group-specific movement probabilities to the NSOG station (Melnychuk 2009a). The two wild groups from 2004 shared one such extra parameter, and the two hatchery groups from 2007 shared another parameter because of small sample sizes of fish detected at QCS and JDF. The two wild groups from 2008 each had their own estimated movement parameter (Fig. A3). These four extra movement parameters were incorporated into the p models (except the general p model, which already allows group-specific p at each station). At NSOG, the estimates of p are not true detection probabilities, but rather joint probabilities of movement and detection.

Assuming the minimum-QAIC_c (best) model, detection probabilities varied widely across receiver stations, for example in 2008, from 0.5%–12.9% at Chk 7 to ~90% at Chk 4, HS_{inner} and HS_{outer} (Fig. A3b). Assuming a linear relationship between $\text{logit}(p)$ and river level, the coefficient for Cheakamus River stations ($\beta_{\text{lev}_{\text{Chk}}} = -4.08$, 95% CI, -5.19 to -2.97) had a steeper slope than for Squamish River stations ($\beta_{\text{lev}_{\text{Sqm}}} = -0.62$, 95% CI, -0.88 to -0.35), although values of these two coefficients may not be directly comparable because of differences in absolute river levels in the two rivers.

Survival probability submodels

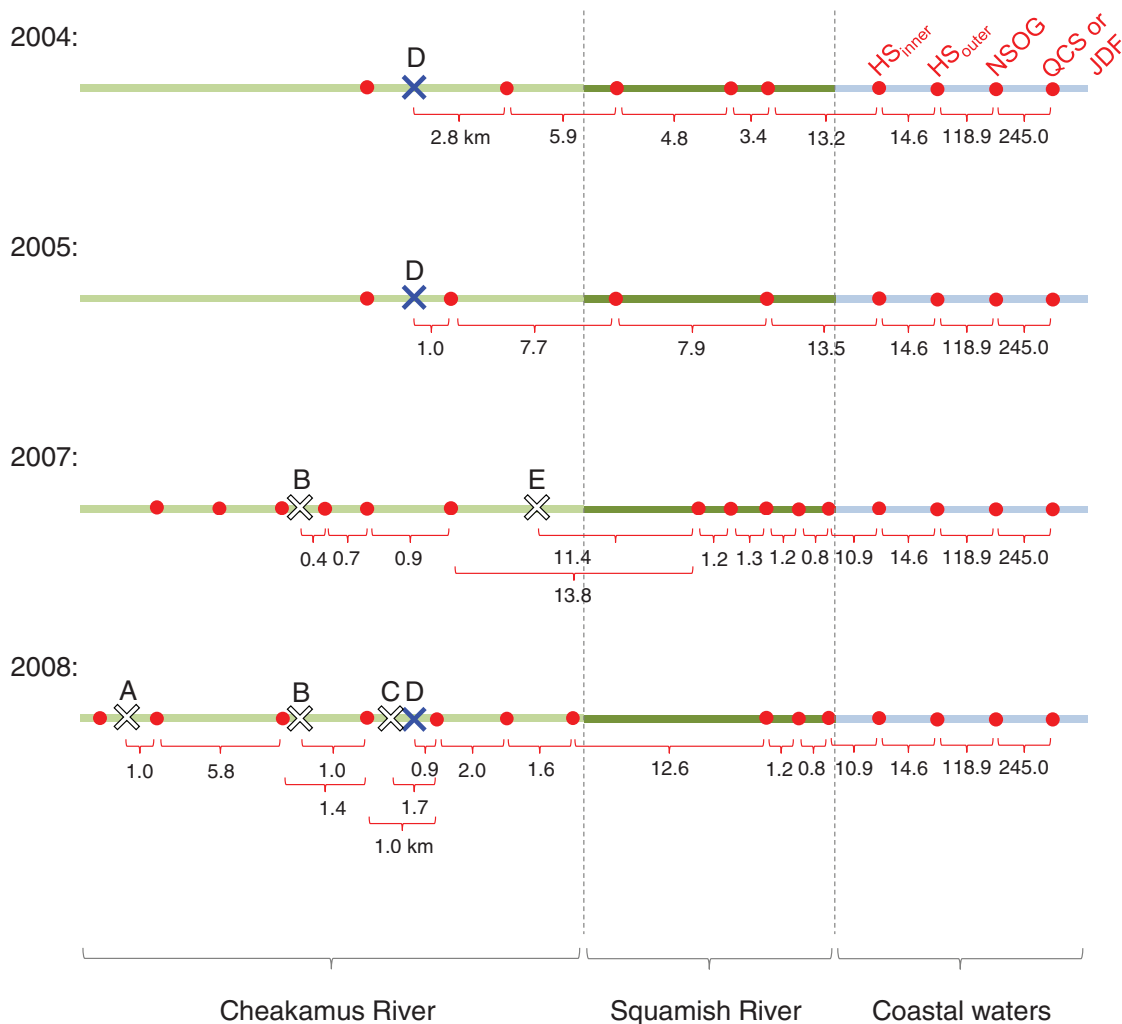
Some survival probability (ϕ) models were based on ϕ being independent in different segments (and years), while others were distance-based, in which segments were related to one another (across years) through the distance covariate on ϕ . Segment

Fig. A1. Daily means of river level in (a) the Cheakamus River and (b) the Squamish River during studies in 2004, 2005, 2007, and 2008. River levels were measured at the Environment Canada gauge station near the Chk 5 (2008) station (Cheakamus River) and near Brackendale, downstream of the Cheakamus River confluence (Squamish River). Release times of tag groups are indicated. River levels are correlated with discharge measurements ($r > 0.99$), with approximate equivalence of 1.0 m = 39 m³·s⁻¹ and 2.0 m = 180 m³·s⁻¹ in the Cheakamus River. For the coloured version of this figure, refer to the Web site at <http://www.nrcresearchpress.com/doi/full/10.1139/cjfas-2013-0165>.



lengths were measured with mapping software as shortest-route distances between receiver stations. In these distance-based models, the interest is not particularly in whether increased migration distance results in decreased probability of survival — that is perhaps obvious if mortality agents like predators are spread out along these migration routes. The issue, rather, is to consider which mark–recapture model structure, segment-independent or distance-based, is more suitable as a framework on which to build hypothesized models of interest involving potential effects on ϕ , such as fork length, release date, or initial mortality. Segment-independent models involve more parameters and consequently allow more flexibility in fitting detection data. Distance-based models are constrained to the assumption that $\text{logit}(\phi)$ is indirectly proportional to segment length, but estimated precision under this framework is typically higher than in segment-independent models. Model selection criteria like QAIC_c can assist in arbitrating between these trade-offs to achieve greater parsimony.

Fig. A2. Schematic of smolt release sites in relation to detection stations during 4 years of study. Circles show detection stations along assumed migration routes from left to right; distances between successive stations are indicated beneath them (not to scale). Smolt release sites are shown by a solid "X" for wild groups and by an outlined "X" for hatchery-reared groups, with labels A–E listed in Table 1. For the coloured version of this figure, refer to the Web site at <http://www.nrcresearchpress.com/doi/full/10.1139/cjfas-2013-0165>.

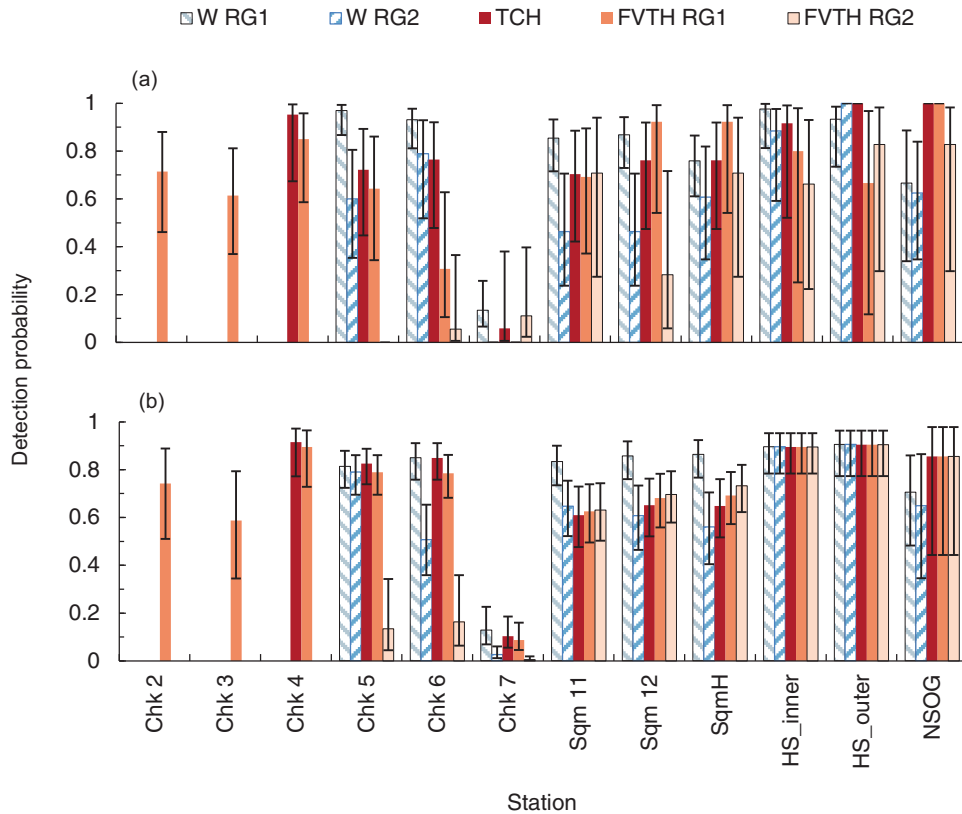


A particular digit of a detection history (e.g., the first or second segment after release) may represent physically different segments for different release groups, even if groups are released in the same river. This can occur if some groups are released further along a migration route than other groups (Fig. A2). One way of dealing with this is to assume conditional independence of survival among segments; smolts from one upstream release location are no more or less susceptible to mortality in some river segment than are smolts in that same segment that were released further upstream (Skalski et al. 2001). This may bias results, however, if any portion of mortality is attributed not only to the particular segment along which smolts migrate, but to how far upstream of this segment they were released. Instead, these differences in physical migration routes were explicitly accounted for in some candidate models; we used additive parameters (on the logit scale) to represent mortality during the first segment after release, wherever the first segment physically occurred. It is appropriate to allow this initial mortality to differ between wild ($M_{\text{initial,W}}$) and hatchery-reared ($M_{\text{initial,H}}$) groups, since hatchery-reared fish may be more susceptible to initial predation mortality, not having been exposed to selection pressures prior to release. These initial mortality parameters also provide a distance-independent initial mortality level for the four distance-based models.

Keeping constant the minimum-QAIC_c (best) model for p from the previous section ($p(S:Y + \text{lev}_{\text{Chk}} + \text{lev}_{\text{Sqm}})$), we compared the nine ϕ submodels on the basis of QAIC_c scores:

1. $\phi(\text{seg};G)$: each release group and each of their segments are fully independent
2. $\phi(\text{seg};Y + \text{FL} + \text{RD})$: ϕ common across release groups in each segment and year; segment and year combinations are independent; additive effects (on the logit scale) of fork length and release date
3. $\phi(\text{seg};Y + \text{FL} + \text{RD} + \text{HW})$: like point 2, with an additive effect (on the logit scale) of HW across all segments and years
4. $\phi(\text{seg};Y + \text{FL} + \text{RD} + M_{\text{initial,H}} + M_{\text{initial,W}})$: like point 2, with additive (on the logit scale) initial mortality in first segment (separate for W and H fish, consistent across years)
5. $\phi(\text{seg};Y + \text{FL} + \text{RD} + \text{HW} + M_{\text{initial,H}} + M_{\text{initial,W}})$: like point 2, with additive effects (on the logit scale) of HW across all segments and years and initial mortality (separate for W and H, consistent across years)
6. $\phi(d_{\text{Chk}} + d_{\text{Sqm}} + d_{\text{sw}} + \text{FL} + \text{RD})$: ϕ_{seg} constrained to segment length, with separate relationships for Cheakamus River, Squamish River, and ocean segments; additive effects (on the logit scale) of fork length and release date

Fig. A3. Estimated detection probabilities at receiver stations in the Cheakamus River, Squamish River, and early ocean portions of smolt migration routes in 2008. Estimates are shown under assumed models: (a) $\phi(\text{seg};G)$, $p(S;G)$ and (b) $\phi(d_{\text{Chk}} + d_{\text{Sqm}} + d_{\text{sw}} + \text{HW} + \text{FL} + \text{RD} + M_{\text{initial,H}} + M_{\text{initial,W}})$, $p(S;Y + \text{lev}_{\text{Chk}} + \text{lev}_{\text{Sqm}})$, shown by release group. Error bars show 95% CI. Detection probabilities were not estimated at the final ocean detection station at QCS-JDF; they were assumed as fixed values. For the coloured version of this figure, refer to the Web site at <http://www.nrcresearchpress.com/doi/full/10.1139/cjfas-2013-0165>.



7. $\phi(d_{\text{Chk}} + d_{\text{Sqm}} + d_{\text{sw}} + \text{FL} + \text{RD} + \text{HW})$: like point 6, with an additive effect (on the logit scale) of HW across all segments and years
8. $\phi(d_{\text{Chk}} + d_{\text{Sqm}} + d_{\text{sw}} + \text{FL} + \text{RD} + M_{\text{initial,H}} + M_{\text{initial,W}})$: like point 6, with additive (on the logit scale) initial mortality in first segment (separate for W and H fish, consistent across years)
9. $\phi(d_{\text{Chk}} + d_{\text{Sqm}} + d_{\text{sw}} + \text{FL} + \text{RD} + \text{HW} + M_{\text{initial,H}} + M_{\text{initial,W}})$: like point 6, with additive effects (on the logit scale) of HW across all segments and years and initial mortality (separate for W and H, consistent across years)

Fork length (mm) was used as an individual covariate. Release date, a group covariate, was coded as number of days since 1 March of the year so that results are not sensitive to leap years in 2004 and 2008.

Comparing factors affecting survival

On the basis of QAIC_c scores (Table 3), there was considerable support for survival models containing covariates with an assumed linear effect on logit(ϕ) compared with the more flexible general model that allowed for separate survival estimates for each release group in each segment of the migration. The minimum-QAIC_c model ($\phi(d_{\text{Chk}} + d_{\text{Sqm}} + d_{\text{sw}} + \text{HW} + \text{FL} + \text{RD} + M_{\text{initial,H}} + M_{\text{initial,W}})$, $p(S;Y + \text{lev}_{\text{Chk}} + \text{lev}_{\text{Sqm}})$) contained several such covariates. Boolean predictor variables included wild versus hatchery rearing and initial mortality parameters in the first segment after release, common across hatchery groups or common across wild groups. Numerical predictor variables included fork length, release date, and per-kilometre mortality constraints with separate slopes between logit(ϕ) and segment length for the Cheakamus River, Squamish River, and ocean segments. We can

compare the relative influence of these factors on survival by looking at estimated coefficients. To place all covariates on a similar scale, the five numerical covariates were each centred and standardized by their standard deviations (the three covariates for segment length — Cheakamus River, Squamish River, coastal waters — shared a common centring and standardization across all segments from the three habitats). With all factors accounted for simultaneously, we found a large relative influence on survival of wild versus hatchery rearing and initial mortality of hatchery steelhead in the first segment after release (Fig. A4). Influences of fork length (positive) and release date (negative) were detected, with 95% CI excluding zero, but were smaller in magnitude than the rearing history effects (Fig. A4). Survival per kilometre was lower in segments of the two rivers than in ocean segments (Fig. A4; survival per kilometre in the Cheakamus River would be lowest overall if initial mortality influences $M_{\text{initial,H}}$ and $M_{\text{initial,W}}$ were included in the estimate).

General model predictions

A general CJS model assumes complete independence among release groups and among each of their migration segments (for ϕ) or stations (for p). Without accounting for heterogeneity among individuals, the general model ($\phi(\text{seg};G)$, $p(S;G)$) is very flexible and provides the best possible fit to the detection data of ones and zeros. Survival probabilities are estimated for each segment of each group, and the product of a group's $\hat{\phi}$ is the estimate of survivorship from release to a particular station, shown in Fig. A5. Two patterns seem immediately evident: (i) there is considerable mortality during the downstream migration, with large declines in survivorship with increasing distance, especially early in the

Fig. A4. Estimated coefficients for survival parameters (i.e., effect sizes of covariates on $\text{logit}(\phi)$ under the assumed model: $\phi(d_{\text{Chk}} + d_{\text{Sqm}} + d_{\text{sw}} + \text{HW} + \text{FL} + \text{RD} + M_{\text{initial,H}} + M_{\text{initial,W}})$, $p(S:Y + \text{lev}_{\text{Chk}} + \text{lev}_{\text{Sqm}})$). Numerical covariates (lower five variables) have been centred and standardized to their standard deviations. Error bars show 95% CI. "Hatchery-reared" is the hatchery effect relative to the wild-reared reference group. $M_{\text{initial,H}}$ and $M_{\text{initial,W}}$ refer to initial mortality in the first segment after release, common across all hatchery (H) or wild (W) groups (respectively), and additive (on the logit scale) to the baseline mortality for groups W or H that apply across all segments; d_{Chk} , d_{Sqm} , d_{sw} refer to per-kilometre mortality constraints with separate slopes for Cheakamus River, Squamish River, and salt water, respectively; FL is fork length; and RD is release date.

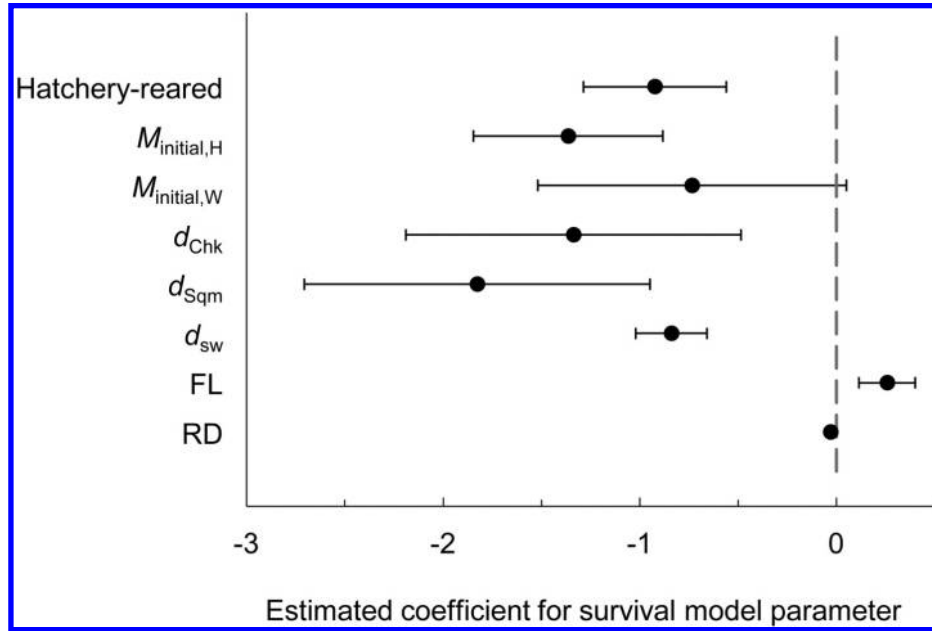


Fig. A5. Survivorship estimates from release to successive detection stations during the smolt migration, prior to adjustment for residualization. Estimates are shown assuming model $\phi(\text{seg}:G)$, $p(S:G)$, plotted against minimum migration distance from release location. Wild groups are shown by circles–squares–diamonds, while hatchery groups are shown by triangles. Error bars show 1 SE. Note that for four release groups not all parameters of the model were well estimated (see Table A1). For the coloured version of this figure, refer to the Web site at <http://www.nrcresearchpress.com/doi/full/10.1139/cjfas-2013-0165>.

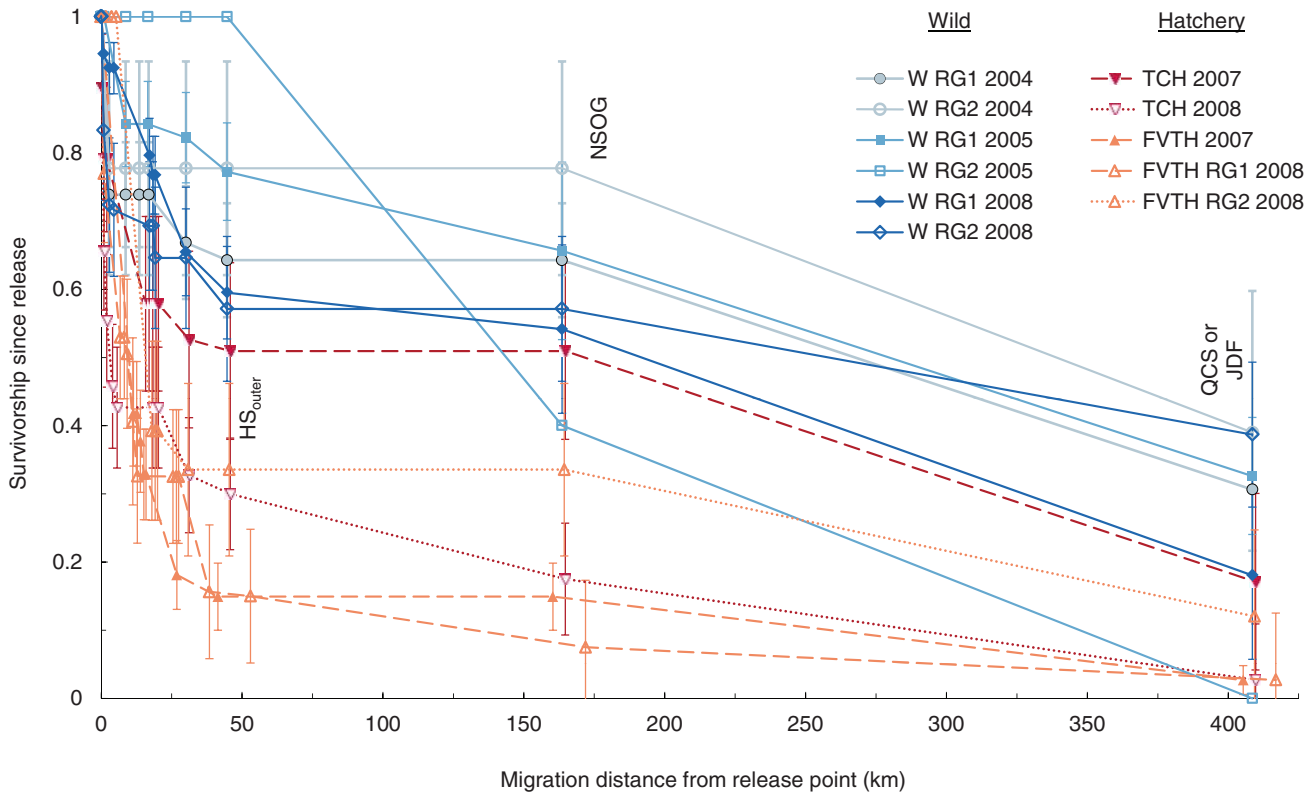


Table A1. Estimated survivorship from release to three detection points during the smolt migration, under two different model assumptions, prior to adjustment for residualization.

Release group	Survivorship (SE)		
	To ocean entry	To HS _{outer}	To QCS-JDF
Model $\phi(d_{\text{Chk}} + d_{\text{Sqm}} + d_{\text{sw}} + \text{HW} + \text{FL} + \text{RD} + M_{\text{initial,H}} + M_{\text{initial,W}})$, $p(S:Y + \text{lev}_{\text{Chk}} + \text{lev}_{\text{Sqm}})$			
W RG1 2004	0.766 (0.034)	0.706 (0.035)	0.291 (0.039)
W RG2 2004	0.704 (0.061)	0.633 (0.070)	0.212 (0.061)
W RG1 2005	0.824 (0.028)	0.763 (0.032)	0.325 (0.043)
W RG2 2005	0.784 (0.036)	0.712 (0.044)	0.258 (0.049)
W RG1 2008	0.720 (0.034)	0.666 (0.039)	0.281 (0.042)
W RG2 2008	0.694 (0.037)	0.637 (0.043)	0.250 (0.046)
TCH 2007	0.364 (0.055)	0.303 (0.056)	0.061 (0.056)
TCH 2008	0.358 (0.048)	0.299 (0.048)	0.060 (0.048)
FVTH 2007	0.308 (0.047)	0.241 (0.045)	0.035 (0.014)
FVTH RG1 2008	0.233 (0.046)	0.192 (0.046)	0.037 (0.046)
FVTH RG2 2008	0.279 (0.052)	0.219 (0.050)	0.032 (0.041)
Model $\phi(\text{seg:G})$, $p(S:G)$			
W RG1 2004	0.739 (0.077)	0.643 (0.084)	0.306 (0.090)
W RG2 2004*	—	—	—
W RG1 2005	0.843 (0.063)	0.773 (0.071)	0.326 (0.086)
W RG2 2005*	—	—	—
W RG1 2008†	0.768 (0.057)	0.595 (0.068)	0.181 (0.123)
W RG2 2008	0.646 (0.104)	0.571 (0.106)	0.387 (0.106)
TCH 2007*	0.579 (0.128)	0.510 (0.130)	0.171 (0.130)
TCH 2008†	0.427 (0.089)	0.300 (0.082)	0.027 (0.082)
FVTH 2007†	0.328 (0.066)	0.149 (0.049)	0.027 (0.021)
FVTH RG1 2008	0.325 (0.098)	0.150 (0.098)	0.027 (0.098)
FVTH RG2 2008*	0.393 (0.131)	0.336 (0.127)	0.120 (0.127)

*Two wild release groups, with <10 fish tagged, had some parameters poorly estimated, at boundaries, and two hatchery groups had <20 fish tagged. Estimates for these four groups under the general model are likely sensitive to sparse data, with imprecise and (or) inaccurate estimates.

†Three groups showed poor goodness-of-fit under the general model (which was assessed with RELEASE), so we interpret their results with caution.

migration, and (ii) in general, wild groups tended to have higher overall survival than hatchery-reared fish, a difference that was established early, soon after release. Two release groups (W RG2 2004 and W RG2 2005) had <10 fish tagged (let alone detected), so parameter estimates under this general model are clearly sensitive to random chance detection events for these groups (Table A1). A simpler, more constrained model as presented in the main text and Fig. 3 is preferred to the general model even if parameter estimates are not as accurate given the data. Reducing the number of parameters typically leads to improved precision in the estimate of any one parameter and less chance of some parameter estimates being sensitive to sparse data. The same argument can be made for two groups that had <20 fish tagged (Table 1, Table A1).

Survivorship estimates assuming the general model are shown in the lower part of Table A1. The goodness-of-fit, assessed using Program RELEASE, was poor for three groups under the general model (FVTH 2007, TCH 2008, W RG1 2008), so we interpret their results with caution, but the survivorship declines of these groups at least appear to be similar to those of other hatchery and wild groups (Fig. A5). Ignoring the two wild groups with insufficient sample sizes to properly estimate parameters, wild survivorship estimates ranged from 65% to 84% to the Squamish River mouth and from 18% to 39% to the outer ocean lines (Table A1; without adjustment for residualization). Ignoring the two hatchery groups with <20 fish tagged that were also susceptible to some parameter estimates being sensitive to sparse data, hatchery survivorship estimates ranged from 32% to 43% from release to the Squamish River mouth and 3% to the outer ocean lines (Table A1). Thus, despite the potential for some parameter estimates being sensitive to sparse data, survivorship estimates to the three stations in Table A1 under this flexible general model are in line with those under the minimum-QAIC_c model. Uncertainty in survivorship

estimates was much higher under the general model (Fig. A5) than the more constrained and more parsimonious distance-based model (Fig. 3), largely a result of having more parameters estimated and thus less certainty in the estimated value of any one parameter. Survivorship declines assuming the more parsimonious distance-based model (Fig. 3) by and large captured the trends of the general model (Fig. A5), with large early survivorship declines in fresh water and higher survival of wild fish.

Mark-recapture assumptions

Typical assumptions of open-population mark-recapture models are reviewed in detail elsewhere (Burnham et al. 1987; Hightower et al. 2001; Lebreton et al. 1992; Pollock et al. 1990; Skalski et al. 2001). The most important of these include the following:

- tagged animals are representative of the population of interest
- fates of individuals are independent of all other individuals with respect to ϕ and p
- probabilities of ϕ in each segment and p at each station are homogeneous among individuals within the groups specified in the model structure (although use of individual covariates like fork length can relax this assumption since variation in ϕ or p among individuals is accounted for explicitly)
- sampling events (or locations) are short relative to intervals between sampling events
- tagged animals are not affected by tagging procedures or implanted tags
- tag loss or failure are negligible

In spatial migration forms of tag-detection studies, it is also important to assume

- detected tags are in live smolts, not in predator stomachs or in dead fish floating downstream past receivers

- all detections in a final (filtered) dataset are legitimate, not false positives
- smolts do not permanently reside between successive receiver stations — they either die during the migration or continually migrate past receiver lines. The possible state of residency is not treated explicitly for estimating survival, so actual survival is underestimated for any populations that have some fish re-sidualizing in fresh water or residing between stations.

In general, survival estimators are fairly robust to the partial failure of assumptions (compared with population size estimators, for example; Lebreton et al. 1992; Pollock et al. 1990; Skalski et al. 1998; Zabel et al. 2005).

Biases in parameter estimates could have occurred if the above assumptions were violated. The possibility of tag-related mortality or tag shedding exists. Even if tag-related mortality in migrating smolts was higher than in tank studies, as long as the effect was similar for wild and hatchery-reared fish, the conclusion of survival differences between them remains robust. Tag failure may have occurred for one late-migrating group, FVTH in 2007, as some fish could have crossed ocean lines after tag batteries expired. Tags in this group were predicted to shut off around 23 July, but three different fish were detected on the HS_{outer}, NSOG, and QCS lines between 22 and 24 July. Survivorship to the outer QCS or JDF lines may therefore have been underestimated for this group (although tag batteries tend to last at least several weeks beyond their predicted expiry dates). No other release group in any year appeared to cross ocean lines after or around the time of tag expiry.

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