

Route-specific movements and survival during early marine migration of hatchery steelhead *Oncorhynchus mykiss* smolts in coastal British Columbia

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ABSTRACT: For migratory species, spatiotemporal variability in movement patterns, such as routes, has the potential to influence survival, but this aspect of movement ecology is poorly understood. For anadromous steelhead *Oncorhynchus mykiss* smolts, little is known about important migratory corridors used during early marine migration. To investigate route-specific movements and survival during outmigration, we implanted acoustic tags into 243 hatchery steelhead smolts, released them at 2 different points along their migration route, and tracked their migration through coastal British Columbia for up to ~400 km. Poorest survival was in the river and the marine inlet first encountered by smolts. Releasing smolts beyond this inlet increased survival to the first marine subarray by more than 2-fold relative to fish released in freshwater. Total survival to the final subarray was 9.1% and 27.3% for river- and marine-release fish, respectively. Survival rates in all other migratory segments were similar between release groups, suggesting that the near-shore environment after ocean entry is a region of particularly low survival for outmigrant steelhead. Route-specific survival was detected through a series of channels ~200 km from release, with the westernmost route being associated with significantly higher survival for smolts. This westernmost passage was also more travelled, with 77% of smolts using this route. Migration rates were higher and more variable through these islands, potentially due to tidal-driven currents in this region. Approximately 11% of tagged smolts exhibited 'milling patterns', including reversals in migration direction or lateral movements along subarrays. Our results demonstrate rare evidence of route-specific survival of a migrant organism and identify potentially important, yet understudied corridors for juvenile salmonids along the British Columbian coast.

KEY WORDS: Migration ecology · Movement ecology · Anadromous fishes · Migration survival · Salmonid smolt · Route-specific survival

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INTRODUCTION

Animal migrations are complex and diverse behaviours witnessed across numerous taxa, including insects, birds, mammals, and fish (Chapman et al. 2014). Migrations can confer various benefits to an individual, including access to favourable feeding areas (Igota et al. 2004, Daly et al. 2014), reproduc-

tive opportunities (Chapman et al. 2012), and a reduction in predation risk (Skov et al. 2013), but movements can also come at a cost. Spatiotemporal variability in movements may have direct implications for an organism's fitness or survival (Nathan et al. 2008). For example, dynamics of the environment, such as barriers to movement, currents, predator density, and resource availability, have the potential

to influence migrations (Alerstam et al. 2003). The interactions of these factors can result in variable migratory behaviours, such as migration routes and timing (Hays et al. 2001, Gschwend et al. 2008, Singh et al. 2012). Such variability can influence an individual's probability of survival (English et al. 2005, Furey et al. 2015, Hewson et al. 2016, Sicurella et al. 2016), but empirical examples remain rare (Holyoak et al. 2008). Linking variation in organismal movements to fitness is at present an understudied aspect of wildlife ecology (Holyoak et al. 2008, Nathan et al. 2008), yet identifying important migratory routes and/or regions may be useful for informing spatial allocation of conservation resources (Hewson et al. 2016) or future industry development along migratory corridors (Sawyer et al. 2009, Cohen 2012). The present study aimed to investigate spatial movements for a migratory species, including how route- and location-specific movements can influence survival for a migratory species.

For migratory anadromous salmonids *Oncorhynchus* spp. in the northern Pacific, population productivity is generally characterized by high interannual variability; however, declines in abundance and survival in many species and populations have been evident since the early 1990s (Irvine & Fukuwaka 2011, Irvine & Akenhead 2013). These declines have prompted considerable research to identify factors influencing productivity of these economically, culturally, and ecologically important species (e.g. Cohen 2012). Productivity of salmonid populations can be linked to the marine phase, particularly during the 'smolt' life stage (Irvine & Akenhead 2013), when fish undergo dramatic physiological changes and migrate from freshwater natal areas to the marine environment. At present, however, the specific factors influencing survival during this critical life-history phase are poorly understood.

Acoustic telemetry studies in the Pacific Northwest have shown that the near-shore marine environment is typically associated with low smolt survival. Survival can vary during the first 300–400 km of marine migration, but generally ranges between ~3 and 30% depending on the species or population (Welch et al. 2009, 2011, Balfry et al. 2011, Clark et al. 2016). Even though smolt losses during this initial marine migration can be a relatively small fraction of the losses incurred at sea prior to returning as adults (Welch et al. 2011), poor survival during the early marine period is underscored by the short timeframe over which it occurs (typically ~2–4 wk as smolts navigate towards offshore feeding grounds (Melnychuk et al. 2010, Welch et al. 2011, Clark et al. 2016). For some

species, such as anadromous steelhead trout *Oncorhynchus mykiss*, this critical period has been linked to declines in both wild and hatchery-based populations in the Pacific Northwest in recent years (Goetz et al. 2015), highlighting the need for a better understanding of the factors influencing survival during this initial coastal marine period.

The Salish Sea is a semi-enclosed marine embayment situated between Vancouver Island and the mainland of British Columbia (Beamish & MacFarlane 2014, Benedict & Gaydos 2015), which forms an important migratory pathway as smolts move from natal rivers to their offshore feeding grounds. Steelhead and sockeye salmon *Oncorhynchus nerka* are typically thought to move through estuaries and the Salish Sea in particularly rapid and highly directed migrations compared with other species of salmonids, which may take up residency for extended periods (Tucker et al. 2009, Melnychuk et al. 2010, Welch et al. 2011). The increased use of acoustic telemetry in recent years has further characterized fine-scale movements of migrating smolts through the Salish Sea. For example, migratory movement patterns and their impacts on survival have been investigated for steelhead smolts at the Northern Strait of Georgia telemetry subarray (spanning between the mainland of British Columbia and Vancouver Island, ~130 km northwest of Vancouver), highlighting route-specific survival trends across this portion of the migration (Furey et al. 2015). Milling patterns have been identified around this subarray, including westward and fully counterclockwise movements (Furey et al. 2015). At present, however, little is known about migratory patterns and survival further along in the migration, where numerous islands and fjords offer the potential for further spatiotemporal variability in smolt migration.

We tracked hatchery-reared steelhead smolts from the Seymour River (North Vancouver, British Columbia) as they migrated nearly 400 km through the freshwater and near-shore marine environment. Previous acoustic telemetry work on this population has suggested that survival is particularly low for smolts migrating through the first marine inlet (~18 km long) encountered on leaving the estuary (Balfry et al. 2011), but sample sizes were low. We used acoustic telemetry with a large sample size of steelhead smolts to quantify survival and movement patterns, and to identify regions and routes associated with poor migratory success. Two release groups were employed to experimentally test the hypothesis that the first marine inlet is a region of particularly low survival for smolts outmigrating from this watershed.

New acoustic receiver subarrays were deployed along the migration route at the northern exit of the Salish Sea and in Johnstone Strait, which provided us with the ability to assess route-specific survival and migration movements for steelhead smolts at finer spatial and temporal scales than previously possible.

MATERIALS AND METHODS

Study system

The Seymour River is a regulated system located in North Vancouver, British Columbia (Fig. 1). Its watershed drains approximately 176 km² (Balfry et al. 2011) and flows south where its mouth meets Burrard Inlet. The Seymour Hatchery is located just downstream

of the Seymour Falls Dam, which blocks historical spawning access to salmonids *Oncorhynchus* spp. in the river. The hatchery produces up to 30 000 steelhead trout annually, which are typically reared for a year and released as smolts in the spring (Seymour Salmonid Society 2015). If released in the Seymour River below the dam, steelhead smolts migrate downstream to Burrard Inlet (~2.5 km from freshwater release site) and then northwest through the Salish Sea, the Discovery Islands, and Johnstone Strait before reaching Queen Charlotte Sound and ultimately the open Pacific Ocean (Balfry et al. 2011, Welch et al. 2011; Fig. 1A). Presently, the hatchery loads smolts onto trucks and releases them beyond Burrard Inlet, in response to a study by Balfry et al. (2011), which suggested this region was associated with poor survival.

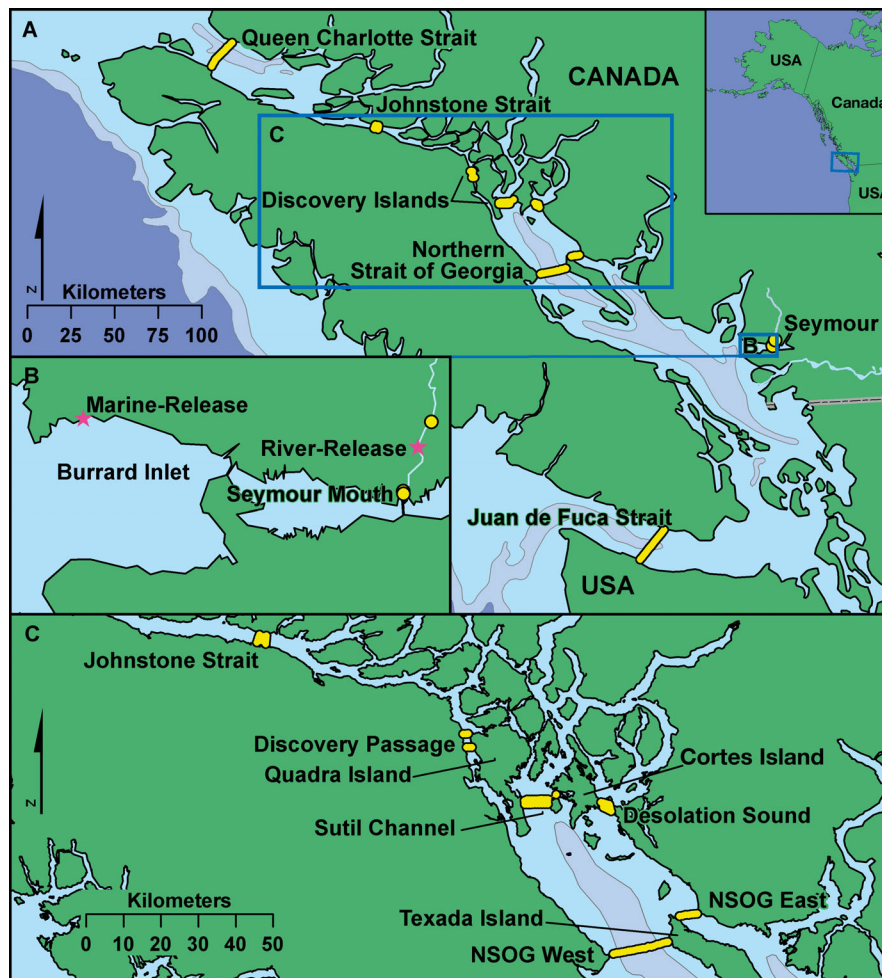


Fig. 1. (A) Study area for Seymour steelhead *Oncorhynchus mykiss* in 2015. Yellow circles and lines represent either individual receivers or a receiver subarray. (B) Close up of Burrard Inlet and Seymour River. (C) Close-up of the Northern Strait of Georgia, Discovery Islands, and Johnstone Strait region. Fish were tagged at the Seymour River hatchery in May, then transported and released at either West Vancouver ('marine-release'; $n = 160$) or the lower Seymour River ('river-release'; $n = 83$), indicated by the stars. The depth contours show the 200 and 500 m isobaths

Acoustic tagging

Tagging took place at the Seymour Hatchery (49° 26' 15.2" N, 122° 58' 01.1" W) on 14 and 15 May 2015. A total of 243 steelhead smolts (fork length [FL] = 200.2 mm [± 0.8 mm SE]; mass [M] = 77.0 g [± 1.1 g SE]; Table 1) were randomly removed from hatchery rearing channels, placed in separated raceways, and restricted from feeding for 24 h prior to surgeries. Surgeries followed Collins et al. (2013) and Furey et al. (2016), and are described in greater detail in the Supplement at www.int-res.com/articles/suppl/m577p131_supp.pdf (see 'Acoustic tagging'). Surgeries took between 1 and 9 min (mean = 3.5 min [± 0.1 min SE]), and surgical instruments were sterilized between each surgery. Following surgeries, fish were placed in separated raceways grouped by release location (i.e. all river-release smolts were grouped together) and allowed to recover for at least 4 d prior to their release. Of the 243 smolts acoustic-tagged (VEMCO V7-2L, 7 mm \times 18 mm, ~ 0.7 g in water; 69 kHz, VEMCO, www.vemco.com), 164 were also non-lethally biopsied using small bone cutting forceps to remove the tips of 2–3 gill filaments for a separate study. Previous studies involving much smaller sockeye smolts (~ 120 mm FL) have suggested no impact on the survival of fish receiving this non-lethal gill clip treatment (Martinelli-Liedtke et al. 1999, Jeffries et al. 2014). Tagging procedures followed the University of British Columbia Animal Use Protocol A15-0205.

Acoustic telemetry infrastructure

As steelhead smolts migrated through the Salish Sea, they passed several marine acoustic receiver subarrays (combination of VEMCO VR2W, VR3, and VR4 receivers) originally designed by the Pacific Ocean Salmon Tracking project (Welch et

al. 2002) and now maintained by the Ocean Tracking Network Canada (Cooke et al. 2011). These subarrays are located in the Northern Strait of Georgia (NSOG), Queen Charlotte Strait (QCS), and Strait of Juan de Fuca. In 2015, 2 new marine subarrays were deployed to investigate marine migration north of the Salish Sea in the Discovery Islands (DI) and Johnstone Strait (JS) region using new dual-frequency (69 and 180 kHz) VR4 receivers (Fig. 1C). In addition, several temporary receivers were deployed in the Seymour River (~ 2.5 km from release). In sum, this large-scale acoustic receiver array (comprising over 100 receivers) allowed tagged smolts to be tracked from their point of release to the northern or southern tip of Vancouver Island (Fig. 1A), an in-water migration distance of up to ~ 400 km.

Fish releases

Tagged steelhead were loaded into ~ 1000 l tanks on trucks and released at 1 of 2 locations: (1) in the lower Seymour River (hereafter, 'river-release') (49° 19' 18.7" N, 123° 00' 50.4" W) or (2) directly into saltwater in West Vancouver (hereafter, 'marine-release') (49° 20' 24.8" N, 123° 13' 58.2" W; Table 1). These 2 release sites (Fig. 1B) were chosen to experimentally test the influence of migrating ~ 18 km through Burrard Inlet on survival to the NSOG subarray. The marine-release group (n = 160) was transported and released on 19 May along with (~ 20000) untagged hatchery-reared steelhead smolts. The river-release group (n = 83) was released over the course of 3 d (21–23 May; ~ 25 – 30 smolts d⁻¹) to minimize acoustic interference between tags, or 'tag collisions' on the lower river receivers and thus improve detection probability. Each river release included untagged conspecifics (~ 200 – 300) to mimic typical hatchery releases.

Table 1. Summary of Seymour River hatchery steelhead *Oncorhynchus mykiss* smolts used for release and for holding study. na = not applicable

Group	Tag type; frequency	Release dates	Mean fork length (SD) (mm)	Mean weight (SD) (g)	Number	Number gill clipped
Lower Seymour (river-release)	V7-2L; 69 kHz	21–23 May 2015	201.7 (15.2)	78.6 (21.0)	83	57
West Vancouver (marine-release)	V7-2L; 69 kHz	19 May 2015	199.4 (13.2)	75.5 (17.0)	160	107
Holding (saltwater)	Dummy V7; na	na	200.2 (14.6)	76.9 (18.1)	63	40
Holding (saltwater)	Untagged	na	197.6 (12.3)	70.7 (15.6)	34	0
Holding (freshwater)	Dummy V7; na	na	196.4 (12.6)	71.0 (13.6)	60	40
Holding (freshwater)	Untagged	na	200.2 (11.8)	74.8 (14.7)	33	0

Holding study

To investigate the impacts of gill clipping and tagging on smolts in freshwater and saltwater, 123 steelhead smolts were tagged with 'dummy tags' (same weight and dimensions as the V7 tags used for released smolts) and given 4 d to recover prior to being transported for holding at the University of British Columbia. Eighty of these smolts were also non-lethally biopsied for gill tissue. Tagged fish were placed in either a saltwater or freshwater 3000 l tank along with a group of untagged conspecifics in each tank (Table 1). The duration of the holding study was 18 d, which approximately equals the expected travel time of steelhead smolts between Seymour River and QCS (Balfry et al. 2011, Welch et al. 2011). Tagging procedures were consistent between the holding study and acoustic tagging surgeries. Fish were fed daily (EWOS Canada, www.ewos.com) and tanks were monitored several times per day for mortalities and tag loss. At the end of the study, all fish were anaesthetized briefly (as per the acoustic tagging procedure; see 'Acoustic tagging' in the Supplement) and FL and mass were measured prior to the fish being returned to tanks.

The change in mean mass and FL for untagged fish in saltwater and freshwater tanks was calculated. Separate 1-sample *t*-tests were used to compare the change in mass and length of tagged fish to the mean change in untagged fish for each tank. One fish was removed from these analyses due to measurement error.

Survival analyses

To estimate segment-specific and cumulative survival of acoustic-tagged smolts during migration, we

used a spatial mark-recapture model approach (e.g. Welch et al. 2009, Clark et al. 2016). Estimates of survival (ϕ), subarray detection probability (p), and their associated variances were calculated using variants of the Cormack-Jolly-Seber (CJS) model for live recaptured animals (Cormack 1964, Jolly 1965, Seber 1965). This model jointly estimates survival and detection probability within a maximum likelihood framework. See the Supplement for comprehensive details of analyses described below.

Survival analyses followed several steps. First, we screened the data for false detections, forming detection histories for each tagged individual, and then assessed goodness of fit of the data to the model. Separate Mann-Whitney *U*-tests were used to assess whether mean arrival dates at marine subarrays (NSOG, DI, JS, and QCS) differed by release groups or between the routes themselves along subarrays (e.g. if mean arrival date differed between Discovery Passage vs. Sutil Channel). Next, we tested whether release location had an impact on ϕ and p to assess whether it was reasonable to estimate only 1 survival parameter for the 2 release groups in each area where migration routes were shared (i.e. NSOG to DI, DI to JS, JS to QCS). There was no evidence of an effect, so for subsequent analyses, all tagged smolts were pooled in the common migration corridor (NSOG to QCS). Finally, we used Akaike's information criterion (AIC) to assess whether FL, tag burden (the ratio of mass of acoustic tag in air to fish mass), and non-lethal gill tissue sampling affected survival. To test these effects, we compared the performance of the base model with 3 other models; each of these models was the same as the base model, but also included an additive effect for 1 of the 3 covariates of interest (Table 2). To account for model selection uncertainty (i.e. similar candidate model weights; Table 2), we model averaged across the 4 models

Table 2. Ranking of Cormack-Jolly-Seber models based on Akaike's information criterion adjusted for low sample size and for overdispersion (QAIC_c) to test the effect of fork length, gill sampling, or tag burden on survival. $\Delta\text{QAIC}_c = \text{QAIC}_c - \text{QAIC}_{c\text{min}}$, where min indicates the QAIC_c for the best model; ϕ = survival; p = detection probability; NSOG = Northern Strait of Georgia; QCS = Queen Charlotte Strait. The base model is indicated in **bold**

Model	No. of parameters	QAIC _c	ΔQAIC_c	Weight
$\phi(\text{release} \times \text{segment}_{\text{Release to NSOG}}^a + \text{segment}_{\text{NSOG to QCS}}) p(\text{site}^b)$	10	542.281	0.000	0.309
$\phi(\text{release} \times \text{segment}_{\text{Release to NSOG}}^a + \text{segment}_{\text{NSOG to QCS}} + \text{fork length}) p(\text{site}^b)$	11	542.30	0.019	0.307
$\phi(\text{release} \times \text{segment}_{\text{Release to NSOG}}^a + \text{segment}_{\text{NSOG to QCS}} + \text{tag burden}) p(\text{site}^b)$	11	542.76	0.478	0.245
$\phi(\text{release} \times \text{segment}_{\text{Release to NSOG}}^a + \text{segment}_{\text{NSOG to QCS}} + \text{gill clip}) p(\text{site}^b)$	11	543.867	1.585	0.140

^aSegment length to NSOG differed by release group
^bOnly river-release smolts were used to estimate p for the estuary receivers

used to test these effects to generate our final estimates of ϕ and p for each migration segment. We then used the segment-specific survival estimates to calculate survival rates per unit time and distance, and cumulative survival estimates from release.

Route-specific use and survival

Along the marine acoustic subarrays (NSOG, DI, JS, and QCS), initial detection counts of smolts were compiled into histograms to assess the distribution of smolts across each subarray. Few fish were detected on the Juan De Fuca line, so no distribution was created for this subarray. We further assessed route-based movements and survival in the Discovery Islands region (Fig. 1C) using a spatial multi-state mark–recapture model. Similar to the CJS model, multi-state models estimate survival (defined as S as opposed to ϕ for CJS models) and detection probability (p), but they also estimate the probability of movement between states (i.e. route use; ψ). We used this approach to test whether steelhead were more likely to migrate through the DI using (1) Discovery Passage (between Vancouver Island and Quadra Island) or (2) Sutil Channel (between Quadra Island and Cortes Island) (Fig. 1C), and whether the 2 routes resulted in different survival. Only 1 fish was detected migrating through Desolation Sound (between Cortes Island and the BC mainland) and thus was excluded from analyses. Route choice was assigned based on the location of last detection on the DI subarray. Six fish detected at the DI were removed from the analysis because they were last detected on NSOG (i.e. they probably did not migrate north). As multi-state models do not perform well near the boundaries of 0 and 1, we also used bootstrapping to gain additional estimates of route-specific survival through the DI.

A similar multi-state model selection approach was used to assess route-specific survival to the DI based on route along the NSOG subarray (Malaspina Strait, to the east of Texada Island versus the Strait of Georgia to the west). For these analyses, route use was assigned based on the location of first detection on the NSOG subarray. To further investigate disproportional route-use around Texada Island, we used a proportional test of the initial receiver detection position for all smolts, while taking into account channel width of the Malaspina Strait relative to the subarray as a whole.

For these analyses, we used R with the package ‘RMark’ (Laake 2013) to construct models using the

program ‘MARK’ (White & Burnham 1999). Model assumptions include equal survival probability, equal probability of detection, and instantaneous sampling. Typically, detection probability and survival at the final subarray (QCS in the present study) cannot be independently estimated as there are no further subarrays along the migration route. One solution is to select a value for detection probability based on knowledge of the area, or performance of subarrays in similar environments (i.e. Welch et al. 2011, Clark et al. 2016). A pilot study involving double-tagged (VEMCO V9-1H and V4-1H acoustic tags) Seymour River steelhead in 2015 allowed us to more accurately estimate detection probability at QCS than has previously been employed (E. L. Rechisky pers. obs.).

Travel and survival rates

Travel times were calculated from release or departure from one subarray to arrival at the next subarray. Departure was defined as the last detection along a subarray, and arrival as the first detection along a subsequent subarray. For river-release fish, the travel time from release to the estuary could not be accurately estimated because fish were randomly released over 3 d. Next, travel rate in all segments was calculated as distance divided by travel time, where distances were measured for each fish as the shortest in-water distance between the central point of each subarray. For the subarrays spanning multiple channels at NSOG and DI, we measured the distance to the central point of each channel and then calculated an average across all detected fish. To assess the influence of individual smolt FL on marine migration rates (in km d^{-1}), separate generalized linear models were run for each segment migrated in common between the 2 release groups (i.e. NSOG to DI, DI to JS, and JS to QCS). To assess the relationship between estuary residence (duration between first and last detections) and survival to NSOG, a binomial generalized linear model was generated with survival from the estuary to NSOG as the binary response and residence time in the river as the explanatory. We tested the significance of the model by comparing the difference in residual deviances between the model and a null model.

To scale survival by distance and time, we converted survival estimates to survival rates. Model-averaged survival estimates were converted to survival rates per day and per km as: $S^{1/d}$, where S = estimated survival and d = the mean travel time (d) or

mean distance travelled (km). Survival rates based on route between DI and JS were also assessed, to take into account the differences in migration distance (and thus expected differences in migration time) between Desolation Sound and Sutil Channel. A detailed description of survival rate analysis can be found in the Supplement (see 'Survival rates').

Milling patterns during migration

We assessed individual smolt behaviour to identify unusual or unexpected migratory behaviours across the marine portion of migration. Smolt migratory sequences were assessed for 2 aspects of milling: (1) 'lateral movements' along a subarray, defined when smolts were first detected in one channel along a subarray, and next detected on another channel along that same subarray (i.e. first detected in Sutil Channel, then detected in Discovery Passage without first being detected at another subarray), and (2) 'reverse migrations,' classified as making a reversal in direction from one subarray to a previous subarray along the migration corridor (i.e. movement going against the generally expected migration direction).

RESULTS

Survival

Estimated segment-specific survival in freshwater (release to river mouth ~2.5 km downstream) was 79% (95% CI: 67–90%). When accounting for the distance of this migratory segment, survival rates here were particularly low: 0% per 100 km (0–0.1% per 100 km). For river-release smolts, subsequent segment-specific survival from the Seymour River mouth to NSOG was 27% (15–44%), while marine-release smolts experienced 65% (54–74%) survival from release to NSOG. For marine-release fish, the survival rate from release to NSOG was 96% d^{-1} (94–97% d^{-1}) compared with 87% d^{-1} (81–91% d^{-1}) for river-release fish travelling between the river estuary and NSOG. When considering survival rates per 100 km to the NSOG array, these differences were more apparent (marine-release: 70% per 100 km [63–77% per 100 km]; river-release: 40% per 100 km [26–51% per 100 km]; Fig. 2).

Although sample size was limited for river-release smolts in the marine environment (Table S2 in the Supplement), there was no evidence that segment-

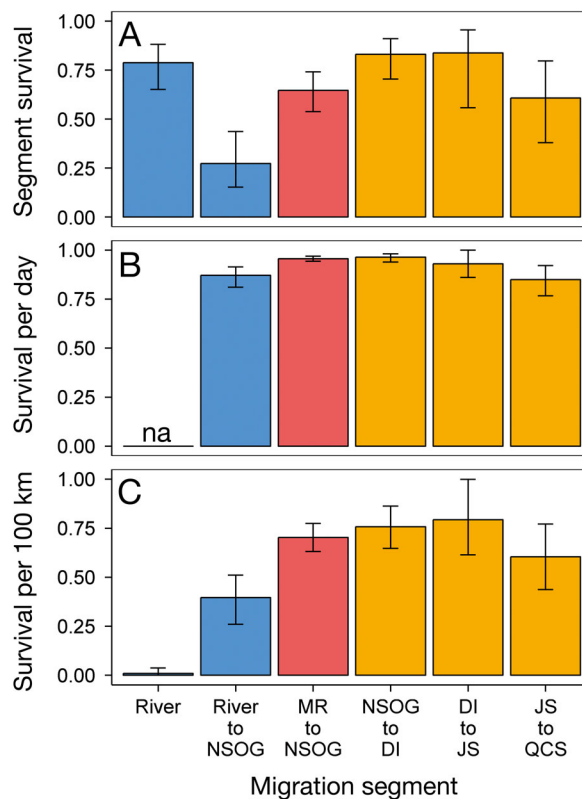


Fig. 2. Model-averaged survival ($\pm 95\%$ CI) for acoustic-tagged steelhead *Oncorhynchus mykiss* smolts (A) per migration route segment, (B) per day, and (C) per 100 km. River- and marine-release (MR) smolts are shown in blue and red, respectively. Estimates to the Northern Strait of Georgia subarray were kept separate for each release group, and were combined for all subsequent detection sites (shown in orange). Survival per day could not be estimated in the river because smolts were released randomly over 3 d, or for marine-release smolts as they were released ~18 km west of the Seymour estuary. na = not applicable; NSOG = Northern Strait of Georgia; QCS = Queen Charlotte Strait; DI = Discovery Islands; JS = Johnstone Strait

specific survival beyond NSOG differed between release groups (Table 3). We therefore pooled release groups from NSOG to QCS to produce one estimate in each of the remaining migration segments. Segment-specific survival increased between NSOG and the DI (83% [70–91%]) and DI to JS subarrays (84% [56–96%]), but decreased slightly in the segment from JS to QCS to 61% (38–80%; Fig. 2). Segment-specific survival estimates are summarized in Table 4. Cumulative survival from NSOG to QCS was 42% (27–57%), and mean survival rates from NSOG to QCS were 70% per 100 km (61–78% per 100 km) and 91% d^{-1} (88–93% d^{-1}). Total survival from release to QCS (~400 km) was 9% (3–15%) for river-release fish and 27% (17–38%) for marine-release fish (Fig. 3).

Table 3. Cormack-Jolly-Seber model selection results of test of whether release groups (release) could be pooled for survival analyses north of the Northern Strait of Georgia (NSOG) subarray. QAIC_c = corrected Akaike's information criteria with low sample size and modified for overdispersion; ΔQAIC_c = QAIC_c - QAIC_{cmin}; QDeviance = model deviance adjusted for overdispersion; QCS = Queen Charlotte Strait

Model	No. of parameters	QAIC _c	ΔQAIC _c	Weight	QDeviance
$\phi(\text{release} \times \text{segment}_{\text{Release to NSOG}}^a + \text{segment}_{\text{NSOG to QCS}}) p(\text{site}^b)$	10	543.585	0.000	0.928	24.793
$\phi(\text{release} \times \text{segment}_{\text{Release to QCS}}^a) p(\text{site}^b)$	13	549.354	5.770	0.052	24.299
$\phi(\text{release} \times \text{segment}_{\text{Release to NSOG}}^a + \text{segment}_{\text{NSOG to QCS}}) p(\text{release} \times \text{segment})$	14	551.550	7.965	0.017	24.390
$\phi(\text{release} \times \text{segment}_{\text{Release to QCS}}^a) p(\text{release} \times \text{segment})$	16	555.282	11.697	0.003	23.892

^aSegment length to NSOG differed by release group
^bOnly river-release smolts were used to estimate p for the estuary receivers

Table 4. Estimates of segment-specific survival, survival rates (per day and per 100 km) and detection probability for each subarray across the study system. na = not applicable; NSOG = Northern Strait of Georgia; DI = Discovery Islands; JS = Johnstone Strait; QCS = Queen Charlotte Strait

Parameter	Release group	Segment	Estimate (%)	SE	Lower 95% CI	Upper 95% CI
Survival (ϕ)	River-release	River	78.8	5.9	65.1	88.1
	River-release	River mouth to NSOG	27.3	7.3	15.3	43.6
	Marine-release	Release to NSOG	64.6	5.3	53.8	74.1
	Combined	NSOG to DI	83.1	5.2	70.4	91.0
	Combined	DI to JS	83.7	9.8	55.8	95.5
	Combined	JS to QCS	60.8	11.3	38.0	79.7
Detection probability (p)	River-release	River	100.0	0.0	0.0	100.0
	Combined	NSOG	81.8	5.0	70.0	89.6
	Combined	DI	94.4	3.5	82.2	98.4
	Combined	JS	71.0	9.4	50.0	85.7
	Combined	QCS	Fixed at 73.0	na	na	na
Survival per day	River-release	River	na	na	na	na
	River-release	River mouth to NSOG	87.1	6.2	75.1	99.2
	Marine-release	Release to NSOG	95.7	3.1	89.5	100.0
	Combined	NSOG to DI	95.4	3.5	88.6	100.0
	Combined	DI to JS	91.3	7.5	76.6	100.0
	Combined	JS to QCS	85.1	6.2	73.0	97.3
Survival per 100 km	River-release	River	0.0	0.0	0.0	0.01
	River-release	River mouth to NSOG	40.4	7.6	27.1	56.1
	Marine-release	Release to NSOG	70.3	4.6	60.6	78.5
	Combined	NSOG to DI	75.7	7.1	59.1	86.8
	Combined	DI to JS	78.8	12.3	45.8	93.9
	Combined	JS to QCS	60.6	11.0	38.7	80.0

Route selection

At NSOG, more steelhead were initially detected in the Strait of Georgia to the west of Texada Island ($n = 63$) than to the east, in Malaspina Strait ($n = 44$; Table S2 in the Supplement). Malaspina Strait is much narrower than the Strait of Georgia, and when accounting for channel width, significantly more fish used the eastern route (width of each channel relative to the width of the subarray as a whole; proportions test, $\chi^2 = 16.504$, $df = 1$, $p < 0.0001$). Use of Mala-

spina Strait was mostly by marine-release fish; only 3 of 15 river-release smolts detected along NSOG were detected in the Malaspina Strait.

Along the DI subarray, fish predominantly were first detected in Discovery Passage ($n = 72$) compared with Sutil Channel ($n = 37$) and Desolation Sound ($n = 2$; Fig. 4). Multi-state model results indicated a transition probability (i.e. probability of route use; ψ) of 77% (64–86%) for Discovery Passage and 23% (13–36%) for Sutil Channel. Smolts showed no indication of skewed distributions of arrival positions

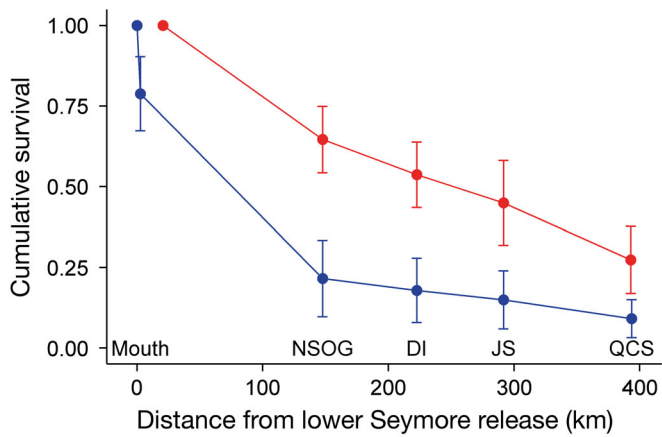


Fig. 3. Cumulative survival ($\pm 95\%$ CI) of steelhead *Oncorhynchus mykiss* smolts from release to the Queen Charlotte Strait (QCS) subarray. River- and marine-release smolts are shown in blue and red, respectively. Mouth = mouth of the Seymour River; see Fig. 2 for abbreviations

along the JS subarray, and a slight tendency for migrating toward the southern shore along the QCS subarray (Fig. 4).

Multi-state model selection results suggested that migration route at the NSOG subarray (i.e. east vs. west of Texada Island) did not influence survival to the DI (Table S1 in the Supplement); however, there is strong evidence that route selection at the DI impacted survival of smolts to the subsequent subarray at JS. The top-ranked model for the segment between the DI and JS considered the 2 routes (Discovery Passage to the west, and Sutil Channel to the east) separately and was strongly supported (97.3% of corrected AIC [AIC_c] weight; Table 5). Survival estimates through Discovery Passage and Sutil Channel to JS were 100% (0–100%) and 47% (19–77%), respectively (bootstrapped estimates: Discovery Passage: 98% [87–100%]; Sutil Channel: 46% [23–72%]). When factoring in the difference in migration route distances and time spent migrating between the 2 routes, survival was estimated to be 97% per 100 km (82–100% per 100 km) for Discovery Passage, compared with 48% per 100 km (24–73% per 100 km) for Sutil Channel. When considering migration time, migration rates were 99% d⁻¹ (92–100% d⁻¹) and 84% d⁻¹ (71–93% d⁻¹) for Discovery Passage and Sutil Channel, respectively. Raw detections can be found in Table S2 in the Supplement.

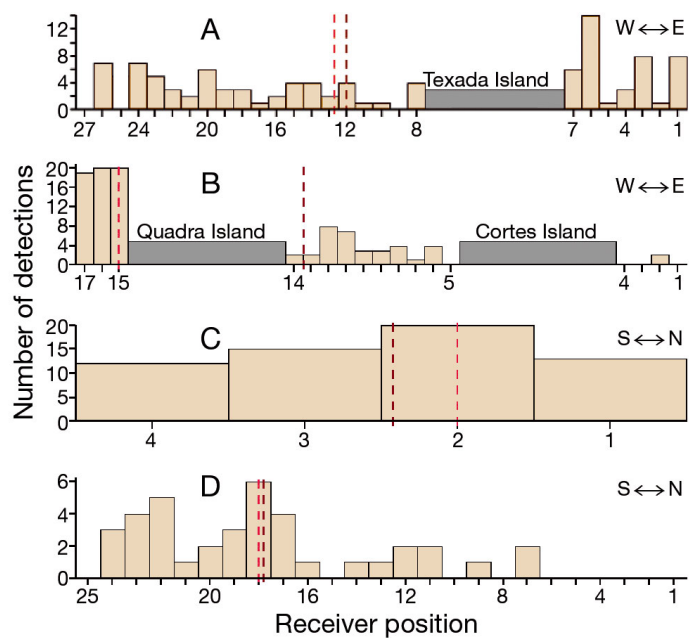


Fig. 4. Distribution of first detections for tagged steelhead *Oncorhynchus mykiss* smolts across the marine subarrays at (A) Northern Strait of Georgia, (B) Discovery Islands, (C) Johnstone Strait, and (D) Queen Charlotte Strait. Values along the x-axis represent individual receiver locations along the subarrays (oriented ~west–east for A and B and ~south–north for C and D), while grey boxes indicate islands interrupting some of the subarrays. As the distributions are of first detections along arrays, the figure does not necessarily reflect the final routes fish used along subarrays (i.e. through the Discovery Islands). Brown and red dashed vertical lines are mean and median of distribution along arrays, respectively

Effect of fork length, gill clipping, and tag burden

When assessing the effects of FL, gill clipping, and tag burden on survival, model selection results revealed similar model weights across all candidate models, including the base model (base model: $\phi[\text{release} \times \text{segment}_{\text{Release to NSOG}} + \text{segment}_{\text{NSOG to QCS}}] p(\text{site})$; Table 2). This base model had the largest weight for any model, with 30.9% of the AIC_c weight. Addition of covariates (FL, gill clipping, tag burden), however, did not greatly improve the amount of deviance explained relative to the base model (Table 2). The model that included FL as a covariate had 30.7% of the AIC_c weight. In this model, the coefficient estimate for FL was slightly positive with a 95% CI spanning zero (0.014 [–0.001 to 0.029]), indicating limited evidence that larger fish survived better than smaller fish. Mean tag burden for acoustic-tagged smolts was low at only 2.2% ($\pm 0.6\%$ SD), and the AIC_c weight for the model that included tag burden was 24.5%. The model containing gill clipping had the lowest model weight at 14.0%. The coefficients for both tag burden and gill clipping in their

Table 5. Multi-state model selection results to test whether survival (S) to the Johnstone Strait subarray was influenced by route selection in the Discovery Islands. QAIC_c = corrected Akaike's information criterion with low sample size and modified for overdispersion; ΔQAIC_c = QAIC_c - QAIC_{c,mini}; QDeviance = model deviance adjusted for overdispersion; NSOG = Northern Strait of Georgia; QCS = Queen Charlotte Strait

Model	No. of parameters	QAIC _c	ΔQAIC _c	Weight	QDeviance
Survival different between routes S(release × segment _{Release to NSOG^a} + route ^c × segment _{NSOG to QCS}) p(site ^b) ψ (segment)	12	573.011	0	0.973	15.851
Survival the same between routes S(release × segment _{Release to NSOG^a} + segment _{NSOG to QCS}) p(site ^b) ψ (segment)	11	580.209	7.198	0.0266	25.143

^aSegment length to NSOG differed by release group
^bOnly river-release smolts were used to estimate p for the estuary receivers
^cThe route parameter was used to provide independent estimates for the channels in the Discovery Islands. All smolts were assumed to have a common migration route (except for differences in release locations) from release to the Discovery Islands. Routes split as fish migrated east or west around Quadra Island (i.e. Discovery Passage and Sutil Channel), then rejoined for the final segment between Johnstone Strait and Queen Charlotte Strait

respective models were negative, with 95 % CIs slightly overlapping zero (mean tag burden: -31.7 [-69.99 to 6.63]; mean gill clip: -0.19 [-0.61 to 0.23]), indicating limited evidence for weak negative effects on survival by both gill clipping and tag burden.

Timing and travel rates

Fish released in the river (between 21 and 23 May) were detected in the estuary between 21 May and 16 June (mean: 27 May [±5 d SD]), highlighting that some individuals remained in freshwater for several weeks (~20 % spent more than 1 wk). Of the detections in the estuary, 52 (of 66 total) smolts were last detected on the farthest downstream receiver. Mean estuary residence time (duration between first and last detections) was 1.1 d (±0.2 d SE). Smolts that remained in the river for extended periods were slightly less likely to survive between the estuary and NSOG than those that moved out of the river much more rapidly (binomial generalized linear model [GLM], $\chi^2 = 10.492$, df = 1, p < 0.01). Initial and final detections of smolts on the river estuary receivers were predominantly observed between sundown and sunrise (Fig. S1 in the Supplement).

Mean travel time from release to QCS was 19.2 d (±1.2 d SE) for marine-release smolts. River-release smolts took an average of 12.8 d (±0.9 d SE) to migrate from the Seymour River estuary to QCS. In the first marine segment (to NSOG), migration rate was similar between release groups, with river-release fish travelling 17.3 km d⁻¹ (±1.9 km d⁻¹ SE) and marine-release fish travelling 17.2 km d⁻¹ (±1.0 km d⁻¹ SE). River-release fish mean arrival date was slightly later at NSOG (Mann-Whitney U-test, W = 1071, p < 0.0001), DI (Mann-Whitney U-test, W = 900, p < 0.0001), and JS (Mann-Whitney U-test, W = 389, p = 0.001) subarrays than for marine-release fish, which was expected given the similar migration rates between release groups, slightly later dates of river releases, and extra time river-release fish took to migrate in freshwater. Along the NSOG subarray, mean arrival dates were slightly later at the Malaspina Strait (Mann-Whitney U-test, W = 392, p < 0.0001), and no differences in mean arrival date was detected among the 3 subarrays spanning the DI (Mann-Whitney U-test, W = 1521, p = 0.082).

Travel rates were fastest in the segment between DI and JS (Fig. 5). Between NSOG and DI, travel rates were 21.4 km d⁻¹ (±5.3 km d⁻¹ SE) and 22.6 km d⁻¹ (±1.5 km d⁻¹ SE) for river- and marine-release fish, respectively. Between the DI and JS subarrays (~80 km distance), travel rates became more variable and mean rates more than doubled, with marine-release fish travelling 41.7 km d⁻¹ (±2.3 km d⁻¹ SE) and river-release fish slightly faster at 54.6 km d⁻¹ (±8.6 km d⁻¹ SE; Fig. 5). For the final segment of migration between JS and QCS, travel rate slowed slightly to 34.5 km d⁻¹ (±1.6 km d⁻¹ SE) for marine-release smolts, and 30.2 km d⁻¹ (±4.6 km d⁻¹ SE) for river-release smolts. FL did not influence migration rate in any migration segment (NSOG to DI: GLM, F_{1,75} = 0.927, p = 0.339; DI to JS: GLM, F_{1,54} = 1.283, p = 0.2624; JS to QCS: GLM, F_{1,25} = 0.017, p = 0.896).

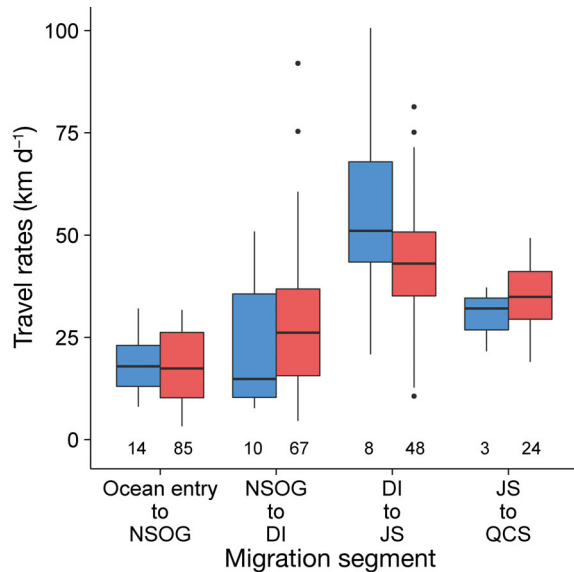


Fig. 5. Segment-specific migration travel rates (km d^{-1}) for river-release (blue) and marine-release (red) steelhead *Oncorhynchus mykiss* smolts. Boxes represent the 1st (bottom) and 3rd (top) quartiles, horizontal lines indicate the median, and vertical whiskers depict maximum and minimum values. Outliers are shown as black dots, and sample sizes are shown underneath each box. Ocean entry represents when smolts left the estuary (for river-release individuals), or were released in the ocean (marine-release individuals). See Fig. 2 for abbreviations

Milling patterns during migration

Of all released fish, 11% ($n = 26$) exhibited milling patterns, such as lateral movements along a subarray or reverse migrations in the marine environment. After release, 5 marine-release smolts were subsequently detected on the Seymour River estuary receivers ~18 km east of the release site (i.e. opposite to the expected migration direction). Only 1 of these fish was later detected on marine receivers as far north as the JS subarray. At NSOG, 2 marine-release fish made lateral movements along the subarray. Only 1 of these fish was a successful migrant to the DI, where it was then classified as a 'reverse migrant' as it was re-detected on the NSOG subarray to the south. All reverse migrations detected within the marine environment ($n = 9$) began somewhere along the DI subarray, with 8 being from the marine-release group. Fifty-five percent of these reversals in migration at the DI began in Sutil Channel, while 45% began in Discovery Passage. Only 3 of these reverse migrants eventually made it back to the DI after re-detection on the NSOG subarray, with none successfully migrating to JS. Fourteen fish made lateral movements along the DI subarrays (marine-release: $n = 12$; river-release: $n = 2$). For these fish,

78% were first detected in Sutil Channel ($n = 11$) and then migrated to Discovery Passage. Eight fish that showed this change in channel migration behaviour made it at least to the JS subarray, and 5 successfully migrated through the system to QCS.

Holding study

At the end of the 18 d holding study, no mortality or tag loss was observed for steelhead in either freshwater or saltwater tanks. Tagging did not affect either final aggregated mean mass in either tank (saltwater: 1-sample t -test, $t_{39} = -0.211$, $p = 0.834$; freshwater: 1-sample t -test, $t_{36} = -0.982$, $p = 0.333$) or final aggregated mean FL in freshwater (1-sample t -test, $t_{36} = -1.320$, $p = 0.195$) of fish. Tagged smolts in saltwater grew slightly larger (~2 mm on average) relative to untagged smolts (1-sample t -test, $t_{39} = 5.003$, $p < 0.001$). Fish were returned to their tanks after the experiment and monitored daily, with no tag expulsion being noted for several months after the study.

DISCUSSION

This study highlights the poor overall survival of hatchery steelhead *Oncorhynchus mykiss* smolts migrating through freshwater and the early marine environment. We tracked steelhead smolts for up to ~400 km and provide further evidence that the early marine period of migration through Burrard Inlet is associated with low survival for juvenile salmonids. Cumulative survival for steelhead trout to QCS (~15–30 d) was only ~9% and ~27% for river- and marine-release groups, respectively. These survival estimates are similar to those estimated in previous years using the same population (Balfry et al. 2011) and are consistent with survival estimates for other stocks and species migrating through the Salish Sea to QCS, including Cultus Lake sockeye smolts (~3–30% survival) (Welch et al. 2009) and Cheakamus River steelhead (27% survival) (Melnichuk et al. 2007).

Within the lower Seymour River, segment-specific survival was estimated to be ~79% from release to the estuary receivers, which is notably low considering this migratory segment represents less than 1% (~2.5 km) of the total distance through the study system. Longer freshwater residency periods were associated with slightly poorer overall survival to NSOG; however, this finding may be a result of survival being associated with time, rather than any specific

characteristic of this landscape. Potential residualization by steelhead (a process where smolts remain in freshwater and do not migrate to the ocean) may have influenced our estimates of freshwater survival, although residualization in hatchery fish is typically ~5% and is least likely when fish are released in small groups close to the estuary (Hausch & Melnychuk 2012), as occurred in our study. In addition, a recent rock slide 2 km upstream of the release site posed a migratory barrier to smolts (S. J. Healy, unpubl. data), and ~80% of final estuary detections were on the downstream estuary receiver, indicating directed movements into the marine environment. Thus, the likelihood of residualization for this population in 2015 was low.

Once beyond the Seymour River, smolts entered Burrard Inlet, which was a region of pronounced poor survival for migrating smolts. This marine inlet accounted for nearly half of the total loss of river-release smolts to the NSOG subarray (~130 km), even though only encompassing ~13% (18 km) of the total distance. In contrast, marine-release smolts, which did not have to migrate through the inlet, experienced ~2.3-times higher survival to NSOG and ~3-times higher survival to QCS (Figs. 2 & 3), indicating that the effect of the high initial losses incurred within Burrard Inlet persisted in the subsequent phases of the marine migration. Survival rates (both per day and per 100 km) to NSOG were also significantly higher for marine-release smolts (Fig. 2), and thus survival differences cannot be simply attributed to a slightly longer migration for river-release smolts alone. Our results therefore support Balfry et al.'s (2011) suggestion that Burrard Inlet is a region of particularly poor survival for Seymour hatchery steelhead.

A lack of receiver infrastructure in Burrard Inlet meant we were not able to assess which direction river-release smolts migrated initially on leaving the estuary. This may have influenced our survival estimates from the estuary to NSOG, particularly if any smolts migrated east (i.e. into a fjord, the Indian Arm) after leaving the estuary. Balfry et al. (2011), who did position receivers farther east of the Seymour River mouth in Burrard Inlet, found that very few smolts (~2–5%) migrated east after leaving the Seymour River estuary, and those that did generally were later detected heading west into the Salish Sea. Even if a similar proportion of our tagged smolts migrated east into Indian Arm and were never detected again, this would still not explain the difference in survival between our release groups to the NSOG subarray. Therefore, we consider that our experimental release groups and receiver subarray setup were effective in

estimating survival for smolts travelling through this marine inlet.

Predation may contribute to the poor survival observed through freshwater and the first marine inlet (i.e. Burrard Inlet). Though we did not directly assess or observe predation, numerous species of birds that prey on juvenile salmonids are prevalent in the area at the time of outmigration, including common mergansers *Mergus merganser*, double-crested cormorants *Phalacrocorax auritus auritus*, and great blue herons *Ardea herodias fannini* (Butler et al. 2015). In the lower Columbia River system, juvenile steelhead are one of the most vulnerable salmonids to predation by waterbirds (Collis et al. 2001), which can account for up to 28% of mortality for outmigrating smolts (Evans et al. 2016). Harbour seals *Phoca vitulina*, which are at carrying capacity in the Strait of Georgia (Olesiuk 1999), target salmon (Yurk & Trites 2000, Thomas et al. 2017) and may be a major source of early marine mortality for outmigrating steelhead smolts in nearby Puget Sound (Berejikian et al. 2016). Other predators, such as Pacific spiny dogfish *Squalus suckleyi*, are common in the broader region and have the potential to prey on smolts and influence survival (Beamish et al. 1992, Beamish & Sweeting 2009). Having never been exposed to predators in a wild setting, hatchery steelhead may be particularly susceptible to predation (Osterback et al. 2014). We detected predominantly nocturnal movements into the estuary by smolts, which is generally considered a predator-avoidance behaviour and has been observed in clear freshwater systems (Chapman et al. 2013, Chase et al. 2013, Clark et al. 2016, Furey et al. 2016). Predation has been hypothesized as a major driver of mortality for other populations of steelhead and sockeye migrating short distances to the sea (Welch et al. 2004, Melnychuk et al. 2007). In nearby Howe Sound (immediately northwest of Burrard Inlet), near-shore mortality of migrant coho salmon *Oncorhynchus kisutch* and steelhead smolts is thought to be influenced by predation 'bottlenecks' (Melnychuk et al. 2013), and such spatial constrictions are also characteristic of Burrard Inlet. Releasing smolts with higher densities of co-migrants may have contributed to an increase in survival to NSOG for marine-release fish, due to a reduction in per-capita predation risk (e.g. 'predator swamping'; Furey et al. 2016); however, we consider any reduction in predation risk associated with co-migrant densities to be small and ephemeral considering the large densities of salmonid smolts migrating through the Salish Sea during this time of year (Peterman et al. 1994, Tucker et al. 2009). Future research could

examine movements of smolts at finer scales and/or investigate predator behaviour and feeding on smolts to help determine why this landscape appears to be a high risk to smolt survival.

Our results provide another example of route-specific survival in migratory species (see Skalski et al. 2002, Perry et al. 2010, 2013, Furey et al. 2015, Hewson et al. 2016). In the DI region, the majority of smolts (~77%) used the westernmost route (Discovery Passage), and those that did benefited by experiencing over twice as high survival to JS (~80 km) as those migrating through Sutil Channel to the east. The Discovery Passage subarray was deployed slightly farther to the north (~18 km) than the other DI subarrays, which may have influenced our estimates of survival, as the distance for this western route to the JS subarray was ~20–25% shorter than those to the east. However, the ~2-fold higher survival advantage for smolts taking Discovery Passage cannot be simply attributed to this difference in migration distance alone. Even when factoring in migratory distance, survival rates per 100 km were still estimated to be approximately twice as high for smolts migrating through Discovery Passage compared with Sutil Channel. We are therefore confident that these differences in route-specific survival are ecologically relevant.

Several factors may be contributing to variable use of migratory routes through the early portion of marine migration. Outmigrating salmonid smolts in the marine environment are thought to orient using Earth's magnetic field (Putman et al. 2014a,b) and make directed migrations toward feeding grounds irrespective of currents (Thorstad et al. 2004, Hedger et al. 2008, Melnychuk et al. 2010). Strong surface currents, however, still influence smolt movements (Booker et al. 2008, Mork et al. 2012); therefore, the migratory trajectories of steelhead smolts are likely a combination of active swimming and the surface currents they experience. Furey et al. (2015) hypothesized that tidal currents in the Salish Sea contributed to westward and even counterclockwise movements observed in ~30–50% of steelhead around the NSOG subarray. Similarly, these same tidal currents (with mean surface currents towards the northwest; Foreman et al. 2012) may be pushing or guiding steelhead smolts to the most western route through Discovery Passage. In tidally driven river delta systems, smolts have been found to select routes with increased flow (Perry et al. 2010, Steel et al. 2013), and if this holds true in the early marine environment, it could explain why Seymour steelhead smolts displayed higher use of Discovery Passage, as this route contains some of

the strongest tidal currents in the region (Foreman et al. 2012).

It is currently unclear what is causing differential survival between routes travelled through the DI. Higher water velocities may contribute to faster migration times and subsequent increase in survival (Steel et al. 2013). Navigation through Sutil Channel or Desolation Sound is more complex due to the presence of numerous islands and fjords (Fig. 1C). Discovery Passage, in contrast, provides a more direct route to the JS and QCS subarrays. When factoring in differences in time spent travelling each route, survival rates per day were still higher for Discovery Passage (~70 km) than for Sutil Channel (~110 km), although with slightly overlapping confidence intervals between the 2 routes, suggesting that the differences in survival between these routes are likely not a result of just migration time alone. Smolts may encounter varying levels of predation pressure (Newman & Brandes 2010, Perry et al. 2010) due to higher densities of seal haul-outs (Berejikian et al. 2016, Thomas et al. 2017) or other predators depending on which route they select. Concentrations of nutrients, phytoplankton, and zooplankton are known to vary within the Salish Sea (Peña et al. 2016), thus influencing availability of food and potentially affecting survival for outmigrating smolts. We did not detect an effect of survival based on route selection at the NSOG subarray, as was found for steelhead smolts by Furey et al. (2015), possibly due to interannual differences in predator abundance or food availability. The spatiotemporal extent of predators and/or food distributions and their influence on smolt survival within the Salish Sea itself are poorly understood and warrant further research.

Our holding study and model selection results suggest that survival was not biased by the acoustic tagging procedure. At the end of the 18 d holding period, we found no evidence that tagging affected smolt survival in either saltwater or freshwater. Studies have generally found minimal or no impacts from acoustic tagging on factors such as swimming performance, feeding, or survival in juvenile salmonids, particularly when tag burdens are kept lower than ~4–6% (Welch et al. 2007, Collins et al. 2013, Neville et al. 2015) as was done in our study (mean tag burden = 2.21%). We detected no tag loss over the duration of the holding study, suggesting that our survival analyses were not biased by smolts shedding acoustic tags while swimming. There was little support for models including the effect of tag burden and gill clipping on survival, consistent with studies suggesting the non-lethal gill clipping procedure has

minimal or no impact on growth or survival of juvenile salmonids (Martinelli-Liedtke et al. 1999, Jeffries et al. 2014). Additionally, there was limited evidence to suggest that FL significantly influenced survival. Regardless, we model averaged across the 4 candidate models including these covariates (gill clipping, tag burden, FL; Table 2), which captures their potential impacts on our estimates of survival.

Mean migration rates for steelhead in the Salish Sea ranged between ~ 15 and 30 km d^{-1} (~ 0.9 – 1.8 body lengths s^{-1}) depending on migration segment, a rate similar to those previously estimated in this region for steelhead (Melnychuk et al. 2010, Balfry et al. 2011) and sockeye smolts (Welch et al. 2009). Between the DI and JS arrays, steelhead smolt migration rates increased and were more variable (~ 25 – 60 km d^{-1} ; Fig. 5), and in some cases approached rates (~ 70 – 100 km d^{-1} ; Fig. 5) comparable to those observed for smolts migrating downstream in large freshwater rivers (Melnychuk et al. 2010, Clark et al. 2016). The increased migration rates observed between the DI and JS is likely a result of the narrow channels strongly directing the migration but may also be influenced by selective tidal-stream transport (e.g. Metcalfe & Arnold 1997). Although the mean flow due to tides is close to zero in this region, tidal currents peak at up to $\sim 4.5 \text{ m s}^{-1}$ in some areas within the DI (Foreman et al. 2012), dwarfing the maximum sustained swimming speeds of the smolts. These rapid currents would allow smolts to travel much faster than is typically estimated in marine waters when they flow in the direction of migration, assuming the smolts were able to at least partially shelter from the effect of the tides when the current runs opposite to their migration direction.

A small subset ($\sim 11\%$) of tagged smolts exhibited apparent milling patterns between NSOG and JS, including reversals in migratory direction and lateral movements along arrays. Steelhead are thought to take relatively rapid and directed migrations towards the open ocean as smolts (Hartt & Dell 1986, Welch et al. 2011), but recently, more complex milling behaviours have been identified for a substantial number of steelhead smolts (30–50%) tracked at the NSOG subarray (Furey et al. 2015). This previous research considered milling at a finer geographic scale (i.e. between individual receivers along a single subarray), which likely accounts for the larger percentage of milling behaviours observed compared with the present study. With the addition of new subarrays in 2015, we found that these milling patterns are still present further along in the migration, particularly at the DI subarray. This could be a result of strong tidal

surface currents influencing migration patterns in this portion of the Salish Sea (Foreman et al. 2012) or other factors such as the distribution of food or predators. For smolts making lateral movements along the DI subarray, 64% of those last detected migrating through Discovery Passage survived to JS. In fact, the only milling patterns at the DI that resulted in a successful migration to QCS were by those fish that eventually migrated through Discovery Passage, further underscoring Discovery Passage as an important migratory corridor. It seems likely that at least some of the observed milling behaviour may have been caused by predation. If a tagged smolt is consumed by a predator, the predator's movements could potentially be tracked while the tag remains in the predator's gut; however, we were unable to assess this directly.

The present study identifies critical regions and important corridors for outmigrating steelhead smolts, and could help inform conservation and management of salmonids migrating through the Salish Sea. Determining important migratory regions and routes for smolts may be crucial for informing future development decisions and allocating conservation resources in the region. We have shown that the freshwater environment and the first estuarine inlet are 2 regions of particularly low survival for smolts, and the brief residence in these regions suggests that piscivorous predators play a large role in impacting smolt survival here. Our results also provide empirical evidence that route selection can influence survival during migration, a concept for which empirical evidence remains rare (Holyoak et al. 2008). Large differences in survival between channels through the Discovery Islands were identified, and most smolts were detected migrating through the more favourable route. Our study signifies that this understudied region is a potentially important corridor for juvenile salmonids in the Salish Sea. As mortality rates in the early marine period are thought to directly impact adult returns and population productivity in steelhead (Moore et al. 2012), our results suggest that route-selection during outmigration could be associated with population-level impacts to survival and productivity. This information underscores the importance of identifying critical regions and predominant migratory pathways for these culturally, ecologically, and economically important species.

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