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Population, habitat, and marine location effects on early marine survival and behavior of Puget Sound steelhead smolts

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Abstract. Steelhead trout (*Onchorhynchus mykiss*) smolts suffer high mortality rates during their rapid migration through the Salish Sea. Among-population variability in mortality rates may reflect (1) genetic fitness variation among populations, (2) freshwater environmental effects on fish condition, or (3) differences in local marine conditions upon seawater entry. A reciprocal transplant experiment was conducted to separate the influence of freshwater effects (combined effects of population and freshwater environment) from effects of local marine conditions on survival of two Puget Sound steelhead populations. Steelhead smolts from the Green River in Central Puget Sound (urbanized and hatchery-influenced) and the Nisqually River in South Puget Sound (less urbanized; no hatchery influence) were tagged with acoustic telemetry transmitters and released back into their natal river or transported and released into the other river. Population of origin had little influence on probability of surviving the migration through Puget Sound. However, smolts released into the Green River had higher survival through Puget Sound (17%) than smolts released into the Nisqually River (6%); the extra 64-km migration segment for the Nisqually-released fish accounted for most of the difference between the two release locations. Neither fork length nor translocation influenced survival, though release date did affect survival of Nisqually population smolts regardless of their release location. Residence time and behavior in the two estuaries were similar, and no effects of population of origin or release date were evident. Marine travel rates also did not differ between populations, release dates, or release locations. This study indicates that mortality occurring in the Salish Sea is likely driven by processes in inland marine environments, more so than intrinsic effects of population or freshwater-rearing environments.

Key words: habitat; nearshore migration; reciprocal transplant; steelhead; survival.

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Introduction

Anadromous salmonid populations experience brief periods during which mortality rates are much greater than those at other life stages (Solazzi et al. 1991, Kennedy et al. 2008). Early in the life cycle, density-dependent competition and predation can cause high mortality for juvenile salmonids as they emerge from gravel nests (Elliott 1990, Zabel and Achord 2004). Days to years later (depending on the species), mortality can also be very high shortly after marine entry (Parker 1968, Fisher and Pearcy 1988, Thorstad et al. 2012, Moore et al. 2015). The processes influencing survival during early marine life, including predation (Pearcy 1992, Thorstad et al. 2012), are too poorly understood to provide meaningful management options for recovery of imperiled populations. Populations migrating through inland marine waters often have substantial mortality rates (LaCroix 2008, Welch et al. 2011, Moore et al. 2015), but the variation among populations tells us little about causes of mortality because population-specific factors are entirely confounded with localized marine factors. Among-population variability in early marine mortality rates may reflect (1) genetic fitness variation among populations, (2) freshwater environmental effects on fish condition, or (3) differences in local marine conditions upon seawater entry. Tracking the behavior and survival of individual salmonids that have experienced contrasting freshwater environments as they migrate through inland marine waters provides the opportunity to understand which factors most strongly influence mortality.

Anadromous salmonid populations vary in fitness-related traits such as body shape (Riddell and Leggett 1981, Doctor et al. 2015), migration timing (Spence and Hall 2010, Spence and Dick 2014), and thermal tolerance (Eliason et al. 2011), which presumably reflect adaptations to their natal freshwater environments and to ocean conditions experienced during marine migrations. Among-population trait variation reflects both adaptive and plastic responses to natural watershed-scale diversity in environmental conditions or constraints (e.g., hydrologic regime: Beechie et al. 2006, Berejikian et al. 2013, temperature regime: Beacham and Murray 1989, Hodgson and Quinn 2002, migration distance: Crossin et al. 2004). For example, population-specific differences in both body size and ocean entry timing in Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Onchorhynchus mykiss*) smolts migrating through the Columbia River estuary partially explained variation in early marine growth rate (Weitkamp et al. 2015), a key factor influencing survival in the ocean (Holtby et al. 1990, Beamish et al. 2004). Freshwater and marine habitats altered by effects of urbanization or other processes may cause a mismatch between locally adapted populations and their current habitats, causing lower survival under current conditions than would occur in an undisturbed ecosystem.

Substantial releases of hatchery-origin salmonids influence natural populations through ecological mechanisms in both freshwater and marine environments (Naish et al. 2008, Rand et al. 2012). Interbreeding with hatchery stocks can shift natural population trait distribution by producing offspring with traits intermediate between parental populations (Seamons et al. 2012, Jones et al. 2015), potentially resulting in reduced survival (Araki et al. 2009). Over several generations, phenotypic traits of a natural population can be largely replaced by those of a hatchery population (Ford et al. 2006). How environmental and hatchery-influenced variability among natural populations of anadromous salmonids influences early marine survival is unknown because population-specific traits and location of marine entry are entirely confounded.

Anadromous salmonids often migrate over long distances and experience diverse freshwater environmental conditions influenced to varying degrees by human activities. Estuarine habitats, in particular, can harbor high contaminant concentrations resulting from industry, urban development, and agriculture (Johnson et al. 2007, Meador 2014). Exposure of juvenile salmonids to organic pollutants can decrease the likelihood of survival via several mechanisms, including increased disease susceptibility (Arkoosh et al. 1998, 2001, 2010), disrupted antipredator behavior (Scholz et al. 2000), and suppressed growth rate (Varanasi et al. 1993, Baldwin et al. 2009). Estuarine channels and nearby lands are often modified to accommodate vessel transportation and port traffic, leading to channel simplification and loss of riparian and wetland habitat. Associated changes in urban estuary habitats may reduce invertebrate availability and foraging opportunities (Bottom et al. 2005). Suspended solids from dredging may clog gill filaments and degraded water quality may alter habitat use through avoidance of low oxygen or high waste conditions (Simenstad et al. 1982). Thus, the condition of migrating smolts may vary with the level of estuary urbanization, potentially affecting subsequent marine survival.

The Puget Sound region has experienced dramatic increases in human population over the past 30 yr, during which time anadromous salmonid populations have declined to the point where Chinook salmon (*Oncorhynchus tswaytscha*) and steelhead trout (*O. mykiss*) have been listed as Threatened under the U.S. Endangered Species Act (Ward 2000, Ruggerone and Goetz 2004, Scott and Gill 2008, Beamish et al. 2010). The level of human development influencing salmon and steelhead habitat varies widely among watersheds (Bilby and Mollot 2008). The Green River (named Duwamish River downstream of river kilometer 19, hereafter referred to as Green-Duwamish River) in the Central Puget Sound (CPS) region of the Salish Sea has severely degraded salmon habitat, while the habitat of the Nisqually River flowing into South Puget Sound is considered much more intact (Shared Strategy 2007). These two river systems also have contrasting hatchery management practices. The Nisqually River has not received hatchery steelhead since 1994 (FishPlants Database, Washington Department of Fish and Wildlife). Hatchery-raised steelhead smolts have been released into the Green-Duwamish River since 1969 (Crawford 1979), and recent genetic tools have been used to show that hatchery-origin parents have contributed to the "wild" population in the Green River (Warheit 2014). Thus, the contrasting conditions in the Green-Duwamish and Nisqually watersheds provide a unique opportunity to test the effects of contrasting freshwater environments on subsequent early marine survival.

In the present study, we attempted to disentangle population-of-origin effects from effects of localized marine conditions on the survival and migratory behavior of Puget Sound steelhead smolts. Here, "population effects" refer to genetic properties of the two populations (including any hatchery influence) and freshwater environmental effects on fish condition until the time of tagging. "Location effects" refer to environmental influences of the brief 19 km post-tagging migration (~3 d) to Puget Sound and marine conditions soon after marine entry affecting survival in different areas of Puget Sound (Fig. 1). To separately account for population and location

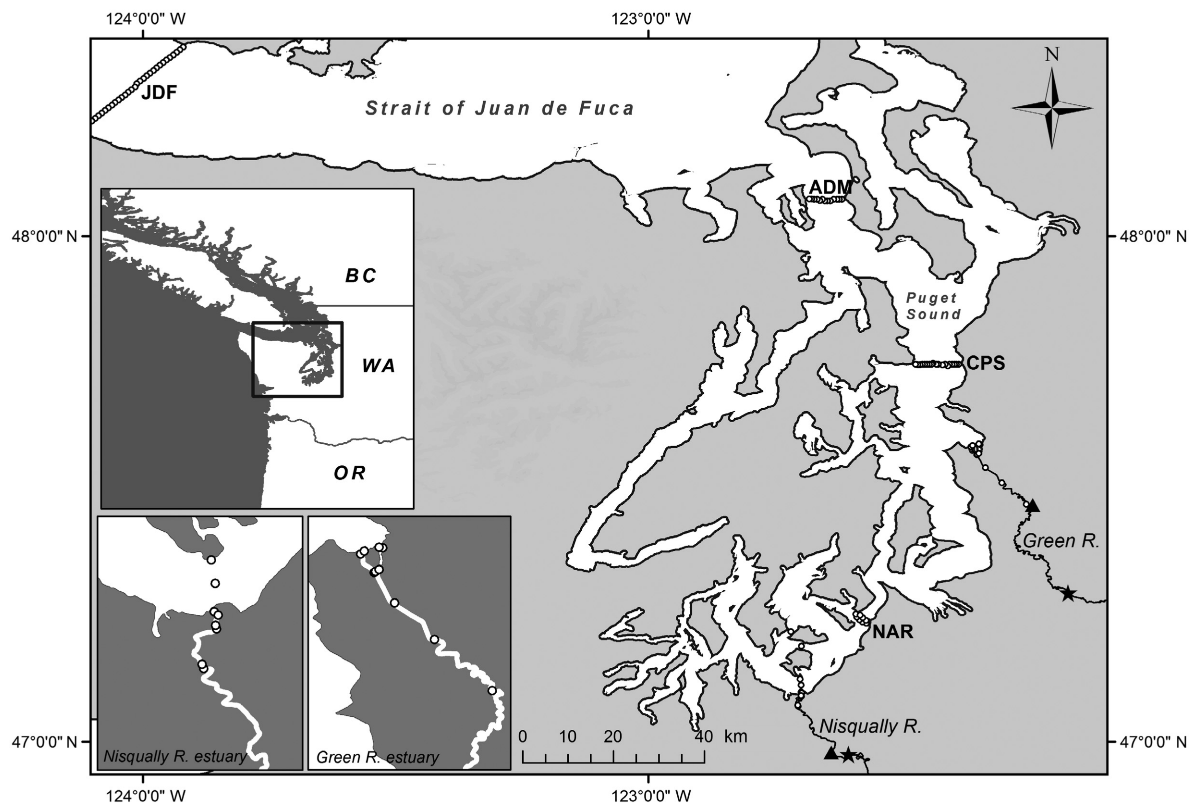

Fig. 1. Puget Sound map showing locations of receivers (open circles) deployed during the steelhead smolt outmigration (NAR = eight receivers in Tacoma Narrows, CPS = 19 receivers in Central Puget Sound, ADM = 12 receivers spanning Admiralty Inlet, and JDF = 30 receivers deployed across the Strait of Juan de Fuca from Pilar Point to near Sooke, BC). Black stars depict the site of smolt trapping on both the Green-Duwamish and Nisqually rivers, and the black triangles represent sites where tagged smolt groups were released.

effects, we performed a reciprocal transplant experiment, wherein steelhead smolts from the Green-Duwamish River in CPS (urbanized and hatchery-influenced) and the Nisqually River (less urbanized; no hatchery influence) natal stream or transported and released into the other system (Fig. 1). Acoustic telemetry receivers were strategically placed to estimate migratory behavior and survival over similar downstream migration distances and in Puget Sound over comparable migration segments.

Methods

Study stream habitat

Land use and quality of habitat differ markedly in the Green-Duwamish River and Nisqually River watersheds. Both banks of the lower 53 km of the Green-Duwamish River are extensively armored and lined with a heavily degraded riparian zone, former meanders have been channelized, and land use in the lower watershed is primarily industrial and residential (Shared Strategy 2007). Below a diversion dam that blocks anadromous fish passage at river kilometer 101, the middle Green-Duwamish watershed is made up of primarily farmland and a mix of urban and rural residential lands. In contrast, the Nisqually River, which enters Puget Sound ~60 km to the south, has only about 5% urban or residential development in the lower 20 km of the river basin. The middle Nisqually watershed is mostly undeveloped with some agricultural and urban land use, with a dam at river kilometer 71 that prevents fish passage into the upper watershed. The riparian zone is considered healthy and the river flows through the largest undeveloped delta in Puget Sound (Shared Strategy 2007).

Smolt tagging

Natural-origin smolts were collected at rotary screw traps on the Green-Duwamish River (rkm 49) and on the Nisqually River (rkm 20) during each of four weeks from 26th April to 23rd May 2014. This date range represented close to the entire typical outmigration period for the Green-Duwamish population, and nearly so for the Nisqually population, though approximately 25% of smolts tend to migrate out of the Nisqually during the first two weeks of June. All smolts were held in flow-through 1.3 m diameter tanks supplied with ambient river water at each trap site for either 1 or 2 d prior to tagging. Logistic regression analysis was used to test for a difference in detections at the Admiralty Inlet receiver array (ADM, Fig. 1) of fish held for 1 d compared to those held for 2 d. Fork length and weight were recorded for each smolt prior to surgery. Between 25 and 28 smolts per week in the Green-Duwamish River (n = 103) and 24–26 smolts per week in the Nisqually River (n = 100) were surgically implanted with VEMCO V7 transmitters (7 mm diameter × 17.5 mm length, 1.4 g, 69 kHz frequency, 30–90 s ping rate; VEMCO, Halifax, Nova Scotia, Canada; see Table 1). Anesthetized smolts (80 mg/L solution of tricaine methanesulfate, MS-222) were transferred to a surgical cradle equipped with a tube continuously administering a maintenance dose of MS-222 (40 mg/L) over the gill tissue. A small incision was made immediately anterior to the pelvic girdle, the tag inserted into the body cavity, and two interrupted monofilament sutures were tied to close the opening. Tagged smolts were then placed in freshwater and typically recovered within 1–2 min. Smolts were held at the tagging location for 20–24 h in flow-through tanks plumbed with ambient river water. The

Table 1. Size and age of tagged steelhead smolts.

Release group	N	Mean length ± SE (mm)	Mean weight ± SE (g)	Age-1 (%)	Age-2 (%)	Number of smolts detected at final receiver line (JDF)*
Green home	53	182.0 ± 2.0	56.3 ± 2.0	49	51	7
Green away	50	178.8 ± 1.8	52.6 ± 1.7	40	53	2
Nisqually home	50	207.2 ± 2.8	84.8 ± 3.8	18	72	2
Nisqually away	50	207.7 ± 3.6	86.9 ± 4.7	18	77	4

Note: Home refers to smolts released into the river from which they were captured and away refers to smolts captured in one river and released into the other.
* Detection probability at the JDF line used in mark–recapture analysis = 68.5%.

study plan and animal care procedures were approved by the NOAA Fisheries Northwest Fisheries Science Center. Half of each group tagged at the Nisqually River was transferred into a 1100-L truck transport equipped with oxygen and driven to river kilometer (rkm) 19 of the Nisqually ("Nisqually home" group), and the other half of the group was transported in the same manner to rkm 19 on the Green-Duwamish River ("Nisqually away" group), where the Green-Duwamish River becomes the Duwamish River. The morning after tagging the Green-Duwamish River smolts, half of the tagged group was transported to the rkm 19 release site on the Green-Duwamish River ("Green-Duwamish home" group) and the other half was transported to the rkm 19 release site on the Nisqually River ("Green-Duwamish away" group). Transport from tagging locations to the "away" release site took similar average amounts of time to both locations (Green-Duwamish to Nisqually: 68 min; Nisqually to Green-Duwamish: 69 min). Average transport times from tagging locations to "home" release sites were also similar (Green-Duwamish: 38 min; Nisqually: 42 min). Care was taken to gradually equalize transport water temperature to ambient river temperature before release. There was never more than a 2°C change between transport temperature and river temperature at release.

Acoustic telemetry receiver arrays

Steelhead smolt migrations were monitored throughout Puget Sound using arrays of acoustic receivers programmed to detect the implanted tags at several locations along the smolt migration path (Fig. 1). Arrays of VEMCO VR2W receivers were deployed near the Nisqually River and Green-Duwamish mouths (six to eight receivers between rkm 0 and 5 in both the Green-Duwamish and Nisqually rivers, two receivers within 2 km of the Nisqually River mouth (RM) in the marine nearshore (km −0.8 and −2.0), and single receivers at rkm 10 and 19 in the Green-Duwamish River) to detect smolts entering Puget Sound and to monitor estuarine behavior (Fig. 1). Additional single receivers were deployed in South Puget Sound in the vicinity of the Nisqually RM to identify nearshore habitat use (Fig. 1). An array of eight Vemco VR3 receivers was deployed 19 km from the Nisqually RM near the Tacoma Narrows Bridge (NAR), and a linear array of 19 VR3 receivers was deployed in CPS 19 km from the Green-Duwamish RM. An additional linear array of 13 VR3 receivers spanned ADM, and a final linear array of 30 VR3 receivers extended across the Strait of Juan de Fuca (JDF) from Pilar Point in Washington State to near Sooke Harbor, British Columbia (Fig. 1). Marine receivers comprising the NAR, CPS, and ADM array were positioned approximately 300 m apart to achieve high rates of detection of the V7 transmitters used in the study. Receivers making up the JDF line were deployed further apart (~750 m), as they were originally deployed to detect larger V9 transmitters. Detection data from VR3 receivers were recovered via surface modem during July (NAR, CPS, ADM) and October (JDF) of 2014. VR2 receivers were recovered and downloaded in June 2014.

Survival and detection probability estimation

Smolt detection data were used to populate Cormack-Jolly-Seber (CJS) mark–recapture models (Lebreton et al. 1992). The models were used to estimate the probability of detection (p) at each receiver array and the probability of smolt survival (φ) through each migration segment. The modeling framework allowed us to evaluate population, release location, release date, and individual body size and condition effects on survival. The R (R Development Core Team 2007) package RMark (Laake 2013) was used to construct φ and p models for the program MARK (White and Burnham 1999). All models incorporated data from the 203 tagged smolts. Goodness of fit of the detection data to the global CJS model was tested using the median $\hat{c}$ method (within MARK), and the variance inflation factors were found to be satisfactory ($\hat{c} \approx 1$). The CJS model cannot distinguish between mortality and emigration, so in this study, $1 - \varphi$ represents both smolts that died and those that did not migrate. However, our data did not suggest any residualism in freshwater, and residency of anadromous *O. mykiss* in marine waters has not been observed in several telemetered populations in Puget Sound (Moore et al. 2015).

Several combinations of factors and covariates were used to construct a series of models to be tested in RMark. Akaike's Information Criteria for finite sample sizes (AICc) were used to identify the set of variables that parsimoniously explained the variation in the survival and detection data (Burnham and Anderson 2010). The model with the lowest AICc was considered the best fit, given the detection data, though models with ΔAICc of less than two were also considered to have substantial support. Models with ΔAICc greater than four have considerably less support, and a ΔAICc greater than 10 suggests a failure of the assessed model to explain substantial variation (Burnham and Anderson 2010). A 95% confidence set of models was compiled by adding up the model Akaike weights from largest to smallest until the sum exceeded 0.95. Estimates of the relative importance of model variables were calculated by summing the Akaike weights across all models in the standardized confidence set where that variable was included (Burnham and Anderson 2010).

Each CJS model was set up to estimate survival through either four or five migration segments, depending on release location: (φ_1) point of release (PR) to RM, (φ_2) RM to either the NAR (smolts released into the Nisqually River) or RM to CPS (smolts released into the Green-Duwamish River), (φ_3) NAR to CPS (Nisqually River releases only), (φ_4) CPS to ADM, and (φ_5) ADM to JDF. Therefore, survival probabilities of smolts released into the Green-Duwamish and Nisqually rivers were compared directly for two separate but congruous segments (φ_1 and φ_2), and φ_3 was deleted from the model for all Green-Duwamish River releases because their migration path did not include a 64-km segment similar to the NAR-CPS segment experienced by Nisqually releases. Survival was compared directly through φ_4 and φ_5, which were identical for all smolts regardless of release location.

The survival probability portion of the CJS models included linear and multiplicative effects of the following factors alone and in combination: (1) Migration "segment" was included in nearly all models to account for environmental differences between segments, (2) population, (3) location, and (4) translocation (home: released into river of origin; away: released into the other river). Interactions between population and location were tested using a "release group" variable. The effect of the longer migration segment for Nisqually-released smolts was not directly tested with the survival models because the extra segment φ_3 (NAR-CPS) for Green-Duwamish released smolts was deleted from the model to enable survival comparison of the first two congruent segments and the last two identical segments. Two individual attribute variables were included in candidate models: length (fork length, mm) and condition factor ("k" = 100 × weight(g)/length(cm)^3), as well as a release date variable (levels = week 1 [27 April–3 May], 2 [4 May–10 May], 3 [11 May–17 May], 4 [18 May–24 May]). The detection probability portion of the candidate models was parameterized to reflect variable p (detection probabilities) for each receiver array because the geometry of the arrays differed substantially.

The CJS model uses detections at subsequent encounter occasions to estimate p for each previous occasion; therefore, φ and p are confounded for the last receiver array. Melnychuk (2009) modeled yearly detection probability JDF estimates (2005–2007 range: 64.1–70.9%) using data from similarly sited and configured receiver arrays spanning the Strait of Georgia in 2005, 2006, and 2007. Thus, we used an average of 2005–2007 values (68.5%) to fix the value of p for the JDF array in our models.

The importance of each variable was assessed relative to the other variables in the analysis using relative weight analysis (Burnham and Anderson 2010). The weight of each modeled variable included in the 95% confidence set (group of top models having a sum of weights ≥0.95) was assessed by summing the weights of each model within which the variable of interest occurred.

Instantaneous mortality rates were compared between migration segments using a distance-based instantaneous mortality rate calculation:

$$(-\ln \varphi_s)/d_s,$$

where φ_s is the model-derived survival probability of a migration segment s, and d is the in-water distance from the beginning to the end of migration segment s.

Behavior in estuaries

The placement of similarly spaced acoustic receivers in the Green-Duwamish and Nisqually estuaries enabled a comparison of smolt behavior in both locations (Fig. 1). Eight receivers in the lower Green-Duwamish River (distance between extreme upstream and extreme downstream receiver = 5.3 km) and six receivers in the lower Nisqually River (4.9 km) were used to calculate one temporal metric ("estuary residence time") and one spatial behavioral metric ("linearity"). Estuary residence time was simply the amount of time in between the first detection at the first upstream estuary receiver(s) encountered and the last detection at one of the last downstream estuary receivers. Linearity served as an index of movement within the estuary receivers' range and was defined as the ratio of the distance between the two farthest apart estuary receivers to the length of a smolt track (sum of all movements between estuary receivers only). A linearity value of 1.0 thus indicates straight line movement in the downstream direction, and any value closer to zero is indicative of a more tortuous track (i.e., having a greater frequency of direction reversals). Estuary residence time and linearity values for each smolt detected on at least two estuary receivers were compared between populations, release location, and release group (Green-Duwamish home, Green-Duwamish away, Nisqually home, Nisqually away) using linear models. A null model for each metric was compared to three additional models representing effects of population, release group, and release location. Response variables were log-transformed to improve normality of the data distribution. Models were compared using AICc (Burnham and Anderson 2010). Additional exploration of estuarine detection patterns in relation to tidal height utilized all estuary receivers, including two receivers located just offshore of the Nisqually RM, and two upstream receivers (rkm 10 and 19) in the Green-Duwamish River (not used in previous analyses because they were not duplicated in both locations).

Travel times and rates

To examine migratory behavior, travel times and travel rates were calculated for the entire early marine migration segment (RM-JDF) and for all individual segments. Travel time was calculated as the time between the last detection at the first detection array in the migration segment and the first detection at the subsequent detection array (only calculated for smolts detected at both lines of a segment). Travel rate was the straight line in-water distance (km) between segment detection arrays divided by the travel time. Effects of population, location, translocation, release date, and fork length on travel rate through the first (PR-RM) and second (RM-NAR/CPS) migration segments were tested using general linear models (insufficient detection information was collected for modeling travel rate through subsequent migration segments). Fourteen candidate models were tested for each segment and were set up to compare the main effects (no interactions) of each variable to solely focus on broad-scale processes. The AICc of each model was then compared to determine the factors that best explained the variation in travel rate using the fewest parameters.

Results

Survival

Steelhead from the Green-Duwamish and Nisqually populations released at both home and away locations survived at similar rates through the freshwater segment (PR-RM), the first marine segment (RM-NAR or RM-CPS), and the CPS-ADM, and ADM-JDF migration segments; the model with the lowest AICc (φ(segment $\times$ release date)) did not specify an effect of population or release location (Table 2). The estimate for φ through freshwater (PR-RM) was high (91.2 $\pm$ 2.0% SE) relative to φ estimates through the marine migration segments (33.8–69.2%; Fig. 2A). The lowest survival probability of any marine segment was estimated for fish released from the Nisqually migrating from NAR to CPS (33.8 $\pm$ 7.0%), a segment not encountered by smolts entering Puget Sound from the Green-Duwamish RM approximately 60 km north (Fig. 2B). Migration through this "extra" segment contributed substantially to the lower overall RM-JDF survival probability of smolts released from the Nisqually River (5.9 $\pm$ 4.2%) compared to smolts released from the Green-Duwamish River (17.4 $\pm$ 7.1%). The modeling results do not reflect this effect of release location because the "extra" segment (NAR-CPS) could not be included in the model for Green-Duwamish releases since those smolts did not encounter such a migration segment. Instantaneous mortality rates were higher in the main basin of Puget Sound (1.5–1.9%/km) than in the rivers (PR-RM; 0.5%/km) and in the Strait of Juan de Fuca (ADM-JDF; 0.7%/km; Fig. 3).

Table 2. Top 20 mark–recapture models in the 95% confidence set, which tested effects of population (pop), release location (location), translocation (trans), release date, length, and condition factor (*k*) on survival through four or five migration segments (depending on release location).

Model rank	Models	Number of parameters	ΔAICc	AIC weight
1	φ(segment × release date)	11	0	0.0454
2	φ(segment + release date)	11	0.0024	0.0453
3	φ(segment)	10	0.1587	0.0419
4	φ(segment + release date + trans)	12	0.5173	0.0350
5	φ(segment + trans)	11	0.8150	0.0302
6	φ(segment × release date + pop)	12	1.1148	0.0260
7	φ(segment + pop × release date)	12	1.1165	0.0259
8	φ(segment + pop + release date)	12	1.1174	0.0259
9	φ(segment × release date + k)	12	1.3392	0.0232
10	φ(segment + release date + k)	12	1.3418	0.0232
11	φ(segment × location)	15	1.5966	0.0204
12	φ(segment × release date + pop + trans)	13	1.6618	0.0197
13	φ(segment + pop × release date + trans)	13	1.6635	0.0197
14	φ(segment + pop + release date + trans)	13	1.6644	0.0197
15	φ(segment + pop)	11	1.6673	0.0197
16	φ(segment × release date + length)	12	1.7255	0.0191
17	φ(segment + release date + length)	12	1.7281	0.0191
18	φ(segment + release date + trans + k)	13	1.8391	0.0181
19	φ(segment × release date + location)	12	2.0691	0.0161
20	φ(segment + release date + location)	12	2.0717	0.0161

Note: All survival portions of the model are paired with a detection probability portion that accounts for differences in *p* for each receiver array (*p*[array]).

Only very small differences in AICc values were seen between that of the null survival model (φ(segment)) and the top mark–recapture models in the survival analysis, indicating a failure of any variable(s) to explain a substantial amount of variation in survival (Table 2). Effects of population, release location, translocation, length, and condition factor on survival were negligible. Release date was included in the survival model with the lowest AICc (φ(segment × release date); Table 2) and explained more variation in survival than the other variables in the analysis (Table 3). Post hoc examination of raw detection data indicated that earlier (late April and early May) migrating smolts from the Nisqually population were detected at a higher rate than later (mid-May) migrating smolts from the Nisqually population, but similar survival rates were observed across release dates for migrants from the Green-Duwamish population (Fig. 4).

Holding time before tagging did not affect survival through Puget Sound. Fish held for 1 d were detected at ADM (Fig. 1) in a similar proportion to those held for 2 d (logistic regression, $t = 0.962$, df = 201, $p = 0.337$).

Estuarine behavior

Migrating steelhead smolts spent an average (±SE) of only 1.09 ± 0.26 d (median 0.25 d; $n = 127$) within range of the Green-Duwamish or Nisqually estuary receivers. Estuary residence time within the Green-Duwamish and Nisqually estuaries was similar among release groups; the null model had the lowest AICc relative to models estimating additional effects of population or release location (Table 4).

Linearity values were very close to one for the majority of tagged smolts ($\bar{x} = 0.93 \pm$ SE 0.02, $n = 187$), indicating unidirectional downstream migration. Linearity values were similar through the two estuaries and did not appear to differ between populations or among release groups (lowest AICc = null model; Table 5). The second best models for both estuary residence time and linearity included only release location and had ΔAICc values of less than 2 (Tables 4 and 5). However, there is little support for the larger

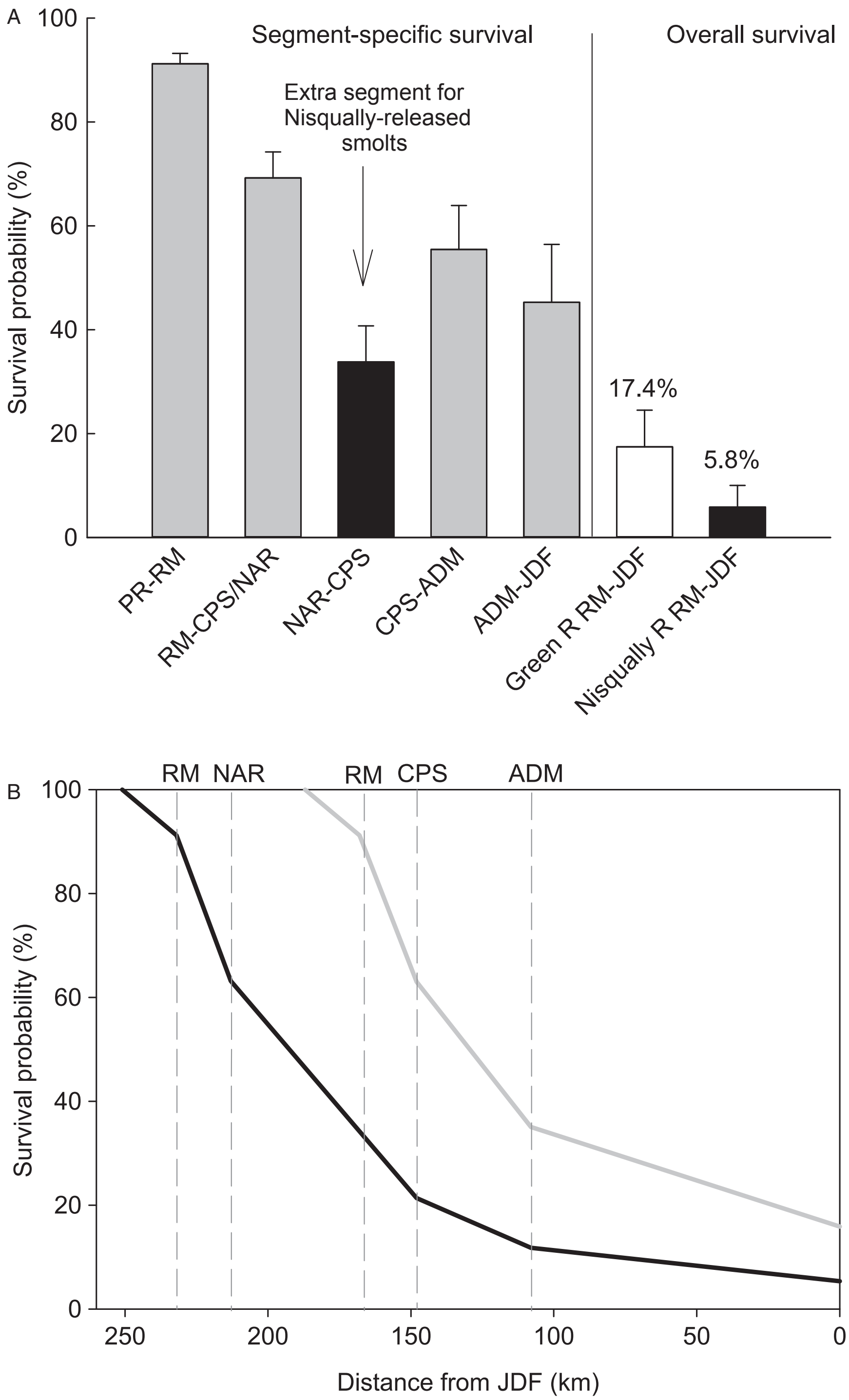

Fig. 2. (A) Estimates of survival probability for all migration segments (PR-RM = Point of release to river mouth, RM-CPS/NAR = river mouth to either the Narrows (Nisqually River releases) or the Central Puget Sound array (Green-Duwamish River releases), NAR-CPS = Narrows to Central Puget Sound array (Nisqually releases only), CPS-ADM = Central Puget Sound to Admiralty line, ADM-JDF = Admiralty Inlet to Strait of Juan de Fuca array) using the mark–recapture model with the lowest AICc (φ(segment × release date)). The final two bars

(*Fig. 2. Continued*)
(Green-Duwamish R RM-JDF and Nisqually R RM-JDF) show survival probabilities as a product of all marine migration segments. Gray bars represent estimates for both Green-Duwamish- and Nisqually-released smolts, black bars represent estimates for Nisqually-released smolts only, and white bars refer to Green-Duwamish River-released smolts only. (B) Survival probability estimates for smolts released from the Nisqually River (black line) and the Green-Duwamish River (gray line) plotted by the distance between the point of survival measurement to the Strait of Juan de Fuca (JDF) receiver array, including survival probabilities estimated at each river mouth (distance from JDF = 232 [Nisqually] and 168 [Green-Duwamish]), at the Narrows (NAR) array (distance from JDF = 212 [Nisqually only]), at the Central Puget Sound (CPS) array (distance from JDF = 148), and at the Admiralty Inlet (ADM) array (distance to JDF = 108 km). Survival probability estimates are derived from the model with the lowest AICc: φ(segment × release date).

model in this case because one additional parameter failed to substantially improve the model fit (Richards 2008, Burnham and Anderson 2010).

Smolts that were known to have survived past the estuaries because of their detection on subsequent receiver arrays (NAR, CPS, ADM, JDF) had very linear paths through the two estuaries (Green-Duwamish = 0.99 ± 0.00; Nisqually = 0.99 ± 0.00) and spent very little time in the estuaries (Green-Duwamish = 0.37 ± 0.03 d; Nisqually = 0.26 ± 0.09 d). None of the smolts with linearity values less than 0.98 (Nisqually River, n = 10; Green-Duwamish River, n = 6), nor those that spent more than 4.4 d in the estuary (Nisqually River, n = 7; Green-Duwamish River, n = 5) were ever detected on any receivers further along the migration pathway (Fig. 5). Thus, smolts with either tortuous paths or long estuarine residence times, or both (most cases), were not successful migrants.

Patterns in the estuary detection data indicate that at least 12 tags may have been detected while in the gut of a swimming predator. Twelve tags assigned low linearity values and above average residence times exhibited direction reversal behavior (Nisqually River, n = 7; Green-Duwamish River, n = 5), where detections were recorded on upstream receivers, then downstream receivers, then subsequently on upstream receivers again (upstream and downstream receivers separated by ≥ 0.9 km). Between 2 and 57 direction reversals were recorded per tag (median = 14). Two additional tags reversed direction just once within the estuary or nearshore. Upstream detections (rkm 4 in the Nisqually River, rkm 10 or 19 in the Green-Duwamish River) of these reversing direction tags were only

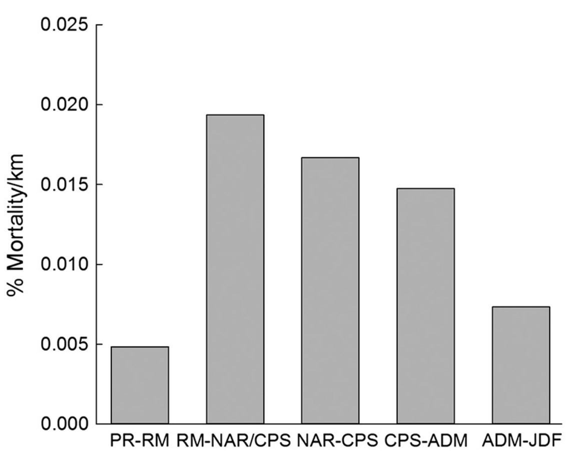

Fig. 3. Instantaneous mortality per kilometer for all migration segments (PR-RM = Point of release to river mouth, RM-CPS/NAR = river mouth to either the Narrows (Nisqually River releases) or the Central Puget Sound array (Green-Duwamish River releases), NAR-CPS = Narrows to Central Puget Sound array (Nisqually releases only), CPS-ADM = Central Puget Sound to Admiralty array, ADM-JDF = Admiralty Inlet to Strait of Juan de Fuca array).

Table 3. Relative importance (sum of Akaike weights) of each variable in explaining variation in survival rates of steelhead smolts.

Model variable	Weight†
Release date	0.677
Translocation	0.331
Population	0.269
Condition factor	0.237
Release location	0.214

† Sum of all Akaike weights in the standardized confidence set (see *Survival and detection probability estimation* section).

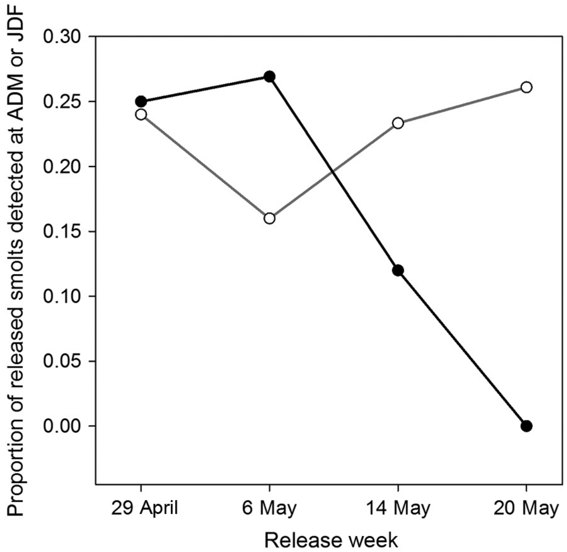

Fig. 4. Percentage of tagged steelhead smolts from the Green-Duwamish population (open circles/gray line) and the Nisqually population (closed circles/black line) detected at either the ADM or JDF array (or both). Detection percentages are calculated from raw detection data, uncorrected for ADM and JDF imperfect detection probability.

recorded at tidal heights above 1.5 m, when sufficient depth was available at upstream locations to accommodate a large swimming predator (Nisqually River head of tide = rkm 4; Green-Duwamish River head of tide = rkm 12; Fig. 6). Nearshore detections near the Nisqually River were only recorded at lower tidal stages (except for tags no. 15843 and no. 15874; Fig. 6).

Travel times and rates

Smolts released into the two rivers took similar average (±SE) amounts of time to migrate from the PR to the RM (Nisqually: 4.04 ± 0.45 d; Green-Duwamish: 3.30 ± 0.34 d; Fig. 6). The PR-RM travel rate model with the lowest AICc (Table 6) included release group and release date. Green-Duwamish Away smolts initially traveled more slowly downriver than the other release groups and then travelled faster when released later, and PR-RM travel time for all release groups generally increased with later release dates. Population, release location, and length variables were not good indicators of PR-RM travel rates (Table 6). After arrival in the estuary, smolts migrating from the Nisqually River that reached the final receiver line (JDF) took an average of only 9.80 ± 1.19 d (n = 4) to travel the 232 km, and smolts released in the Green-Duwamish River traveled 168 km in an average of 8.80 ± 0.44 d (n = 7; Fig. 7).

Travel rates increased slightly after arrival at the estuaries (Fig. 7). Travel times through all migration segments were similar for both populations released in both rivers, and travel rates tended to increase as smolts approached the Pacific Ocean (Fig. 7). Variation in travel rates through the first marine segment (RM-NAR or RM-CPS) was not explained well by any of the variables included in the analysis. The null model had the lowest AICc, and the second and third best models had only one variable (release date and body length, respectively; Table 7). Travel rate varied somewhat by release date, but no clear linear trend was evident.

Table 4. Estuary residence time model comparison.

Model	Number of parameters	ΔAICc	AIC weight
Intercept only	2	0	0.50
Release location	3	1.10	0.29
Population	3	2.04	0.18
Population × release location	5	5.20	0.04

Table 5. Linearity model comparison.

Model	Number of parameters	ΔAICc	AIC weight
Intercept only	2	0	0.54
Release location	3	1.73	0.23
Population	3	2.06	0.19
Population × release location	3	4.82	0.05

Discussion

Green-Duwamish River smolts released in the Nisqually River and Nisqually River smolts released in the Green-Duwamish River in 2014 survived at rates very similar to smolts migrating from their natal rivers, providing no indication that population effects account for variation in the marine survival of these two populations. Nisqually smolts tended to be older at smoltification (higher percentage of age-2 smolts) and were

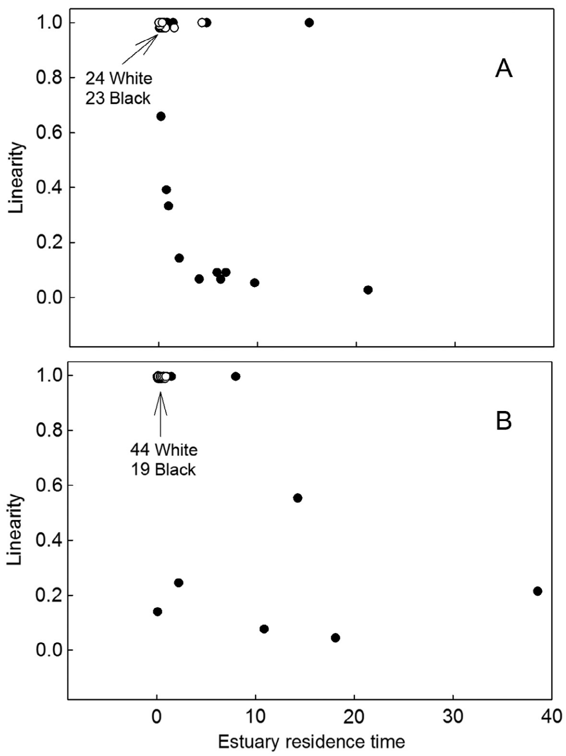

Fig. 5. Linearity values plotted with the estuary residence times for each smolt released in the Green-Duwamish River (A) and the Nisqually River (B). White dots indicate smolts that were detected at a receiver array located farther along the migration path than the estuary (NAR, CPS, ADM, or JDF), while black dots represent smolts that were not detected at any receivers after estuary detection.

longer and heavier on average than Green-Duwamish River smolts. The substantial differences in body size and age may reflect adaptive (i.e., genetic) differences between the populations or phenotypically plastic responses to different river conditions. The similarities in marine survival rates of the two populations, despite measurable phenotypic variation and level of hatchery influence (Green-Duwamish River supplemented since 1969, Nisqually River not supplemented since 1994), indicate that early marine survival rate variation (Moore et al. 2015) may be more regulated by local conditions encountered during their respective early marine migrations. Furthermore, the degree of urbanization in the two rivers differed markedly, yet survival rates from release to RM were indistinguishable in our analysis, and consistent with the conclusion that subsequent marine survival was more strongly regulated by conditions in the marine environment than by freshwater variables.

Marine entry location had a greater effect than population of origin on marine survival. The most parsimonious mark–recapture models did not distinguish between survival probabilities in the first migration segment (RM to NAR or RM to CPS) whether smolts were migrating through South Puget Sound (location of marine entry for Nisqually releases) or through Elliott Bay (location of marine entry for Green-Duwamish River releases), and survival was also similar through common migration segments (CPS-ADM and ADM-JDF). These survival similarities between populations and release locations suggest that marine mortality processes were similar in each initial migration segment and acting independently of processes operating during freshwater life history stages. Smolts released in the Nisqually River suffered substantial mortality during the extra 64-km migration segment (NAR-CPS). The extra distance traveled by smolts emigrating from the Nisqually River resulted in an 11% absolute decrease in overall marine survival probability from RM to the JDF (6%) compared to smolts emigrating from the Green-Duwamish River (17%). Previous multi-population comparisons showed that Hood Canal and Puget Sound populations with longer migration distances tended to survive at lower rates than populations with shorter distances (Moore et al. 2010*a*, 2015). Inner Bay of Fundy Atlantic salmon smolts with longer migration distances to the ocean consistently survived at lower rates than intermediate and outer Bay of Fundy populations (LaCroix 2008). Populations with longer migration distances often take more time to reach the same point than populations situated closer to the ocean, so it is difficult to determine whether time or distance has a greater impact on survival patterns. However, Nisqually-released smolts took an average of about 10 d to reach the JDF array compared to about 9 d for Green-Duwamish River migrants, for which RM-JDF survival was nearly three times greater. Thus, similar travel times for both release locations resulted in substantially different survival rates, indicating that distance likely had a greater

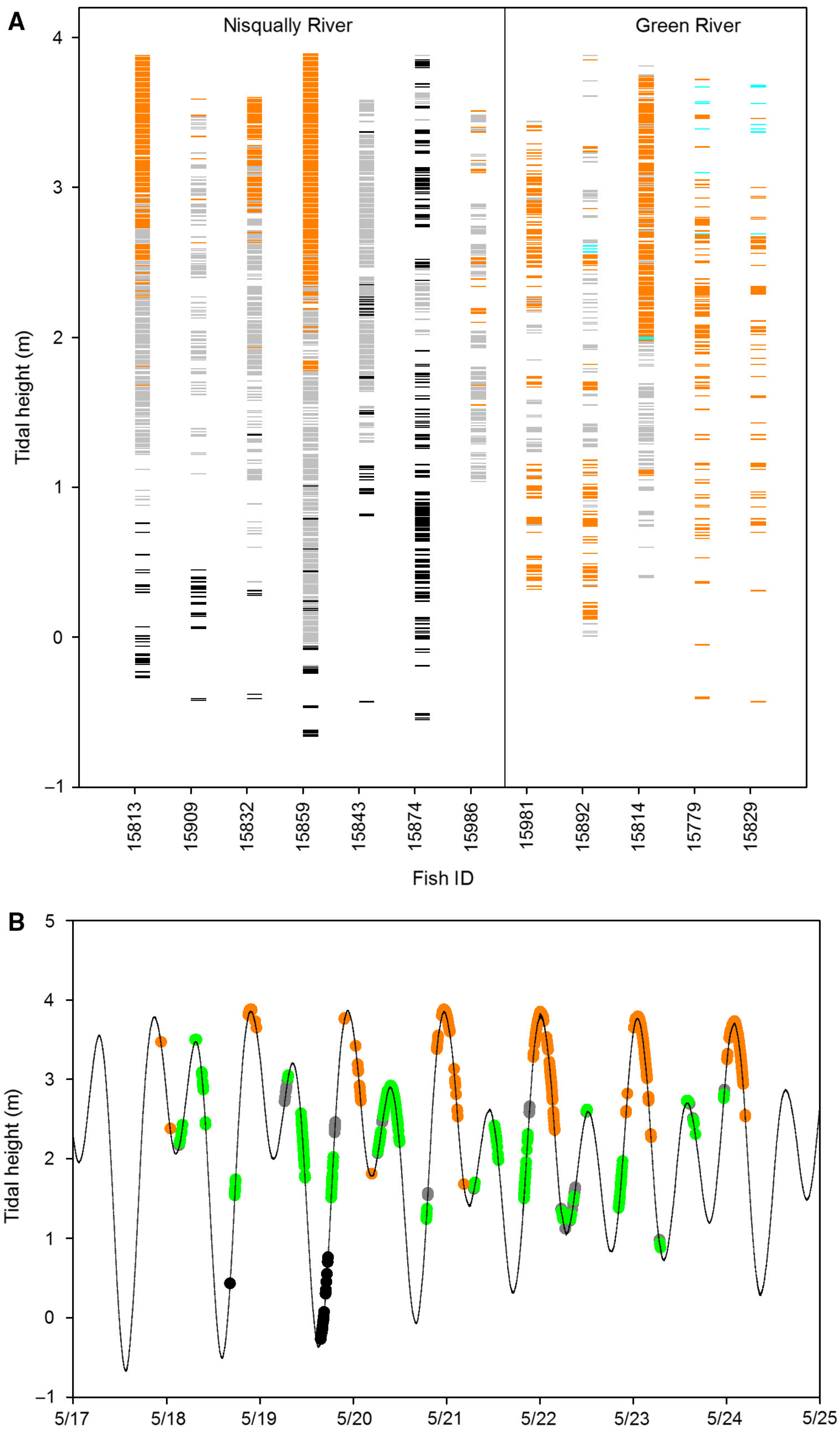

Fig. 6. (A) Detections of 12 acoustic tags released into the Nisqually River (left) and Green-Duwamish River

(*Fig. 6. Continued*)
(right) exhibiting more than two direction reversals within range of any estuary (rkm 0–3 = gray bars, rkm 4–5 = orange bars, rkm 10 or 19 = blue bars) or nearshore (rkm = −0.8 or −2.0; black bars) receivers, plotted by tidal height in meters. The head of tide is located at approximately rkm 5 of the Nisqually River and at rkm 19 in the Green-Duwamish River. (B) Example of direction reversal behavior, shows detections of tag no. 15813 by estuary receivers (rkm 0.2 = gray circles, rkm 1.1 = green circles, rkm 4.0 = orange circles) and nearshore (rkm = −0.8 or −2.0; black circles) in relation to tidal height.

impact on survival rate than did the amount of time spent migrating.

Smolts from the Nisqually River population survived at a higher rate near the beginning of the outmigration (late April) than in later weeks, and by the last release week, no smolts were detected surviving to JDF (Fig. 4). In contrast, the odds of survival were fairly constant across release weeks for smolts from the Green-Duwamish River population (released in either location). This pattern was evident for Nisqually smolts released in both the Nisqually and Green-Duwamish rivers, so was independent of release location. However, the biggest differences in survival over time for both release groups occurred in overlapping segments. For Nisqually fish released in the Green-Duwamish River, we observed decreasing survival rates for groups released from late April to mid-May in the first 19-km marine segment (i.e., between the RM and the Central Puget Sound, RM-CPS), and the most drastic declines in the Nisqually home smolt survival occurred in the migration segment between the Tacoma Narrows and the CPS (NAR-CPS). There may have been some factor unique to the central region of Puget Sound that caused increased mortality of Nisqually smolts during later migration periods. It is also plausible that disease afflicting the Nisqually smolts played a role in increasing smolt mortality in mid-May. During the time of this reciprocal transplant study, *Nanophyetus salmincola*, a parasitic trematode present in South and CPS rivers, was found in high prevalence (97.5%) with high mean intensity (1798 metacercaria/posterior kidney) in steelhead smolts sampled before saltwater entry in the Nisqually River. Smolts sampled in the Green-Duwamish River exhibited a lower infection rate (13.3%) and had a lower mean parasite load (698 metacercaria/posterior kidney) (M. F. Chen et al., *unpublished manuscript*). *Nanophyetus salmincola* infection can decrease swimming ability of infected salmonids (Butler and Millemann 1971), potentially causing some unexplained interaction between infection intensity and release date that may explain the difference in effect of release date between populations.

Table 6. General linear modeling results comparing the effects of experimental and biological factors on travel rate from the point of release to the river mouths.

Models	Number of parameters	ΔAICc	AIC weight
Release group + release date	6	0	0.48
Release group + release date + length	7	2.13	0.17
Population + release date	4	3.04	0.11
Release date	3	3.44	0.09
Location + release date	4	3.94	0.07
Location + release date + length	5	4.57	0.05
Population + release date + length	5	5.01	0.04
Length	3	35.67	0
Release group + length	6	36.31	0
Location + length	4	36.76	0
Population + length	4	37.45	0
Release group	5	37.59	0
Population	3	39.36	0
Intercept only	2	41.77	0
Location	3	42.81	0

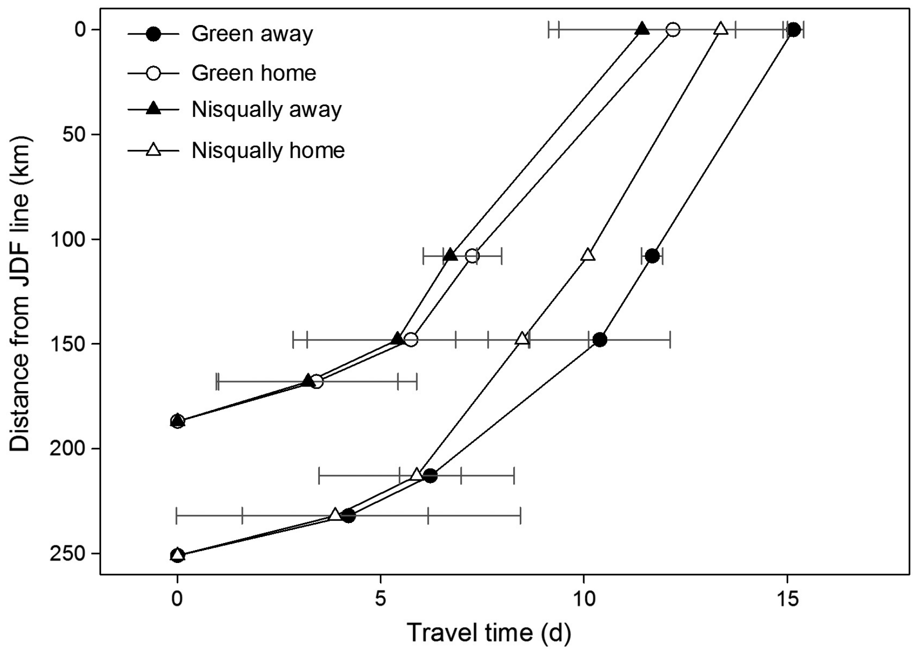

Fig. 7. Mean time (±SE) taken by Green-Duwamish away (closed circles), Green-Duwamish home (open circles), Nisqually away (closed triangles), and Nisqually home (open triangles) release groups to travel from point of release (PR; km 251 for Nisqually River releases and km 187 for Green-Duwamish River releases) to receiver array locations along the migration path.

Table 7. General linear modeling results comparing the effects of experimental factors and body size on travel rate from river mouths (RM) through the first marine segment (Green-Duwamish RM to Central Puget Sound and Nisqually RM to Narrows receiver line).

Models	Number of parameters	ΔAICc	AICc weight
Intercept only	2	0	0.17
Release date	3	0.59	0.12
Length	3	0.60	0.12
Location	3	1.32	0.09
Location + length	4	1.64	0.07
Location + release	4	1.83	0.07
Population	3	2.13	0.06
Population + length	4	2.15	0.06
Release group	5	2.44	0.05
Release group + release date	6	2.45	0.05
Population + release date	4	2.84	0.04
Location + release date + length	5	3.01	0.04
Release group + length	6	3.52	0.03
Population + release + length	5	3.63	0.03
Release group + release date + length	7	4.33	0.02

Pathogen effects, if any, were manifested after smolts entered the marine environment.

Despite substantial differences in the degree of urbanization, migration behavior through the Green-Duwamish and Nisqually estuaries was remarkably similar. Smolts from both populations released in both locations spent similar amounts of time migrating through the lower five km of each river and exhibited very linear paths. This similarity in behavior through both estuaries indicates that estuarine habitat does not play a substantial role in determining the length of time or movement patterns of steelhead in Puget Sound estuaries. Meador (2014) found that hatchery-reared Chinook salmon released into contaminated streams survived at a reduced rate relative to similarly raised Chinook released into more pristine streams. The present study and previous estimates (Moore et al. 2010*a*) indicate that steelhead smolts spend more time in freshwater streams and less time in the estuaries (<36 h) than all other North American *Oncorhynchus* species (c.f. Quinn 2005), except perhaps for cutthroat trout which have similar freshwater residence times but occupy estuaries to a much greater extent (Moore et al. 2010*b*). Therefore, steelhead smolt condition should be much more impacted by freshwater habitat conditions, including water quality, and less impacted by conditions in urbanized estuaries. Our analyses did not detect any variation in survival or migration behavior despite apparent differences in contaminant loads between the two watersheds. Although less urbanized, tissue sampling performed in 2014 found high levels of polybrominated diphenylethers (commonly used in flame retardants) in Nisqually steelhead caught at rkm 20 and in the estuary (M. F. Chen et al., *unpublished manuscript*). Samples from the same study found elevated levels of polychlorinated biphenyls in Green River steelhead caught in the river and estuary, but lower polybrominated diphenylether levels. Water quality aside, differences in the proportion of intact natural habitat also seemed to have little effect on tagged steelhead behavior. The short amount of time steelhead smolts spend transiting estuaries may limit the impacts of water quality or other conditions that may be harmful to other species with longer residence times.

Steelhead smolts entering Puget Sound from the Green-Duwamish River had a higher survival probability (17%) through Puget Sound (RM-JDF) than smolts entering from the Nisqually River (6%). Both of these early marine survival estimates are low and likely limit the productivity of both populations. Previous telemetry studies of Puget Sound and Hood Canal steelhead estimated similarly low early marine survival rates ranging from 13% to 39% during a high survival year (2006) and from 5% to 11% in a poor survival year (2009) (Moore et al. 2015). Steelhead smolts migrating through the nearby Strait of Georgia via Howe Sound (230–350 km) survived at a similar rate (27%) in 2004 and 2005 (Melnychuk et al. 2007), and Atlantic salmon smolts from two inner Bay of Fundy, Canada rivers, survived their nearshore outmigration at rates ranging from only 3–8% over 230 km (LaCroix 2008). Common to both the eastern and western U.S. coasts, salmonid population declines in the last three decades have been linked to reduced marine survival (Ward 2000, Welch et al. 2000, LaCroix 2008, Gibson et al. 2011), and marine survivals are lowest in the first few weeks relative to the remaining time at sea (Hansen and Quinn 1998, Melnychuk et al. 2007, Halfyard et al. 2012, Moore et al. 2015). The present study further confirms these patterns and suggests that the mortality agents in inland marine waters may currently limit productivity of steelhead and other anadromous salmonid species.

It is possible and even likely that the survival probabilities estimated here using acoustic telemetry methods are biased to some degree, as unknown tag effects cannot be quantified. Stress caused by the tagging procedure or the increased weight of the transmitter may make smolts more vulnerable to predation than untagged smolts or cause delayed mortality, thus negatively biasing population survival estimates. Tag loss through the body cavity has also been known to occur, though this process took longer than 21 d to occur in a study of hatchery steelhead smolts tagged with V7 transmitters (Sandstrom et al. 2013), a longer period of time than it took for 100% of the smolts in this study to reach the JDF line. Though survival estimates may not be perfectly representative of the untagged steelhead populations sampled, we can assume that tag effects were equal among treatment groups, so the patterns and relative survival estimates between populations and release groups are unaffected by any tag bias.

Predation is a likely mechanism causing mortality of steelhead smolts in Puget Sound given their high mortality rate over a short period of time (less than 2 weeks on average to travel from RM to the Pacific Ocean). Predation has been implicated in other locations along the Pacific Coast of North America. Telemetry studies conducted in Oregon documented high rates of predation and the presence of marine mammals and birds as tagged coho and steelhead migrated through coastal estuaries (Johnson et al. 2010, Clements et al. 2012). The very tortuous paths (10 documented in the Nisqually River, six documented in the Green-Duwamish River) and long estuary residence times (seven documented in the Nisqually River, five documented in the Green-Duwamish River) of some tags in both estuaries are more indicative of tags in the guts of predators than in living steelhead smolts, and suggest some predation occurring in both of the estuaries studied here. Predator behavior can be contrasted to the behavior of tagged prey using quantitative behavioral parameters (Romine et al. 2014, Gibson et al. 2015). Using similar diagnostics, we collected movement data on estuary receivers to yield insights into possible predators. Low linearity values resulted from sequential detection at upriver, then downriver, then upriver receivers (i.e., back-and-forth behavior), and were never coupled with detection at a receiver array farther along the migratory route out to the ocean. Therefore, back-and-forth behavior was not a behavior associated with a successful steelhead migrant. Multiple daily upriver migrations, however, are characteristic of harbor seal behavior (e.g., Wright et al. 2007). Back-and-forth patterns in the detection data are not likely to have been made by an avian predator because the tags were consistently underwater, and the absence of these back-and-forth detections at upriver sites during low tides suggests that the predator was restricted by shallow water. The other likely marine mammal predator in Central and South Puget Sound, harbor porpoise, is known to use deeper water habitats (Raum-Suryan and Harvey 1998). The anomalous tag detection patterns observed in the monitored estuaries are more consistent with the behavior and known habitat preferences of harbor seals than those of any other predators present in the ecosystem.

Recent research within the Salish Sea ecosystem has documented substantial habitat overlap and inferred predation by harbor seals on salmon and steelhead. Berejikian et al. (2016) used seal-mounted receivers and Global Positioning System (GPS) loggers to quantify and locate interactions between the 203 steelhead smolts tagged in the present study (plus 43 additional tags programmed differently) and harbor seals in Puget Sound. They reported 37 steelhead detections by four harbor seals tagged in CPS, seven steelhead detections by seven North Puget Sound harbor seals, and at least nine steelhead apparently consumed by harbor seals based on the locations of stationary tags near harbor seal haulouts. Thomas (2015) used DNA and hard parts analysis to identify prey remains in harbor seal scat, finding that juvenile steelhead made up roughly 3% of harbor seal diet in the Strait of Georgia in 2012. Given the large energetic requirements of harbor seals and their substantial abundance in the Salish Sea (~14,000 estimated in greater Puget Sound [Jeffries et al. 2003] and 40,000 estimated in the Strait of Georgia [DFO 2010]), a prey population comprising only a small percentage of an individual seal's diet could still be heavily impacted, especially if that population is depressed. Harbor seal populations in the Salish Sea have increased since the inception of the Marine Mammal Protection Act in 1972 (Jeffries et al. 2003), potentially creating what Marshall et al. (2015) termed a "protected predators vs. protected prey" management conflict between seals and Endangered Species Act-listed steelhead. Future research will focus on estimating a predation rate for harbor seals on steelhead smolts migrating out of Puget Sound rivers, to determine the magnitude of harbor seal impact on steelhead survival rates and develop multi-species management measures.

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