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Multi-population analysis of Puget Sound steelhead survival and migration behavior

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ABSTRACT: Until recently, research on mortality of anadromous fishes in the marine environment was largely limited to estimates of total mortality and association with group characteristics or the environment. Advances in sonic transmitter technology now allow estimates of survival in discrete marine habitats, yielding important information on species of conservation concern. Previous telemetry studies of steelhead *Oncorhynchus mykiss* smolts in Puget Sound, Washington, USA indicated that approx. 80% of fish entering marine waters did not survive to the Pacific Ocean. The present study re-examined data from previous research and incorporated data from additional Puget Sound populations (n = 7 wild and 6 hatchery populations) tagged during the same period (2006–2009) for a comprehensive analysis of steelhead early marine survival. We used mark-recapture models to examine the effects of several factors on smolt survival and to identify areas of Puget Sound where mortality rates were highest. Wild smolts had higher survival probabilities in general than hatchery smolts, with exceptions, and wild smolts released in early April and late May had a higher probability of survival than those released in early and mid-May. Steelhead smolts suffered greater instantaneous mortality rates in the central region of Puget Sound and from the north end of Hood Canal through Admiralty Inlet than in other monitored migration segments. Early marine survival rates were low (16.0 and 11.4% for wild and hatchery populations, respectively) and consistent among wild populations, indicating a common rather than watershed-specific mortality source. With segment-specific survival information we can begin to identify locations associated with high rates of mortality, and identify the mechanisms responsible.

KEY WORDS: Steelhead · Survival · Smolts · Migration · Telemetry

INTRODUCTION

The life cycle of anadromous salmonids involves a number of discrete habitats, within which mortality occurs. Different combinations of biotic and abiotic processes control mortality during the embryonic stages in the gravel, throughout life as free-living juveniles in lotic and lentic freshwater environments, along migration routes, and at sea prior to return as adults (Quinn 2005, Jonsson & Jonsson 2011). The majority of lifetime mortality typically takes place during the freshwater stages, but the mortality at sea is substantial, variable among years, and occurs later in the life cycle, so there are fewer opportunities for compensation compared to mortality that occurs during earlier, freshwater stages (Bradford 1995, Quinn

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2005). Most studies of marine mortality have investigated (1) environmental factors related to 'smolt-to-adult' survival (Mantua et al. 1997, Coronado & Hilborn 1998), (2) patterns of survival or recruitment over various spatial areas (Pyper et al. 2005, Sharma et al. 2013), (3) scale growth patterns to assess size-selective mortality (Ward et al. 1989, Holtby et al. 1990, Henderson & Cass 1991, Moss et al. 2005), or (4) the effects of specific predators on populations of interest (Beamish et al. 1992, Willette et al. 2001). More recently the use of sonic transmitters and receiver stations has helped to partition mortality associated with initial entry into the marine environment from that which occurs at later stages (e.g. Halfyard et al. 2013, Lacroix 2013, Melnychuk et al. 2014).

Telemetry studies have been useful in estimating smolt mortality via specific routes and migratory segments (Perry et al. 2013, Romer et al. 2013), and describing smolt migratory behavior within and among populations (Plantalech manel-la et al. 2011, Renkawitz et al. 2012). To reveal ecosystem-scale processes influencing smolt survival, it is important to assess variation in migratory behavior and survival of smolts among habitats, populations, and years. Large-scale comparisons of both geographically similar and more distant populations can help determine whether mortality vectors are local or shared throughout the ecosystem. Furthermore, patterns that emerge from multiple years of study are more likely than patterns from single year studies to reflect consequential as opposed to transient effects on survival. In this study, we report the results of a multi-year, multi-population study examining patterns of migration and survival of steelhead, the anadromous form of rainbow trout *Oncorhynchus mykiss*, in riverine, estuarine, and marine waters of Puget Sound, a fjord complex unique in North America in its combination of physical features and human development.

Marine survival rates (smolt-to-adult returns [SARs]) of steelhead smolts originating in Washington State and British Columbia have declined substantially in the last 25–30 yr (Ward 2000, Scott & Gill 2008). While SARs from populations originating along the Pacific Ocean coast of Washington have increased in recent years from very low levels in the early 1990s, populations from Puget Sound and the greater Salish Sea region (the complex of inland marine waters including Puget Sound, the Strait of Georgia, and associated other straits and inlets) continue to experience low SARs (N. Kendall unpubl. data). Puget Sound steelhead were listed as threatened under the US Endangered Species Act in 2007 (NOAA 2007). The early marine experiences of steelhead smolts depend on where they enter marine waters. Coastal steelhead populations experience ocean conditions immediately upon saltwater entry, whereas steelhead smolts originating in the Salish Sea experience an inland marine ecosystem much more influenced by terrestrial and freshwater processes. Unless steelhead from coastal populations migrate to different ocean regions, some aspects of the inland sea migration likely explains the observed difference in coastal and Puget Sound SARs.

Very low early marine survival through Puget Sound was documented for steelhead from populations that enter Hood Canal (Moore et al. 2010, Moore et al. 2012) and from the Green River (Goetz et al. 2015), which feeds the main basin of Puget Sound. The goal of the present study was to combine telemetry data from these Hood Canal and Green River studies with data from 3 additional Puget Sound populations (the Nisqually, Puyallup, and Skagit rivers) for a more comprehensive regional survival analysis. We investigated temporal, biological and geographic factors that may affect survival of steelhead smolts, comparing the performance of wild and hatchery-reared fish over 4 years. By comparing survival rates among populations and examining spatial patterns of mortality, we sought to identify specific sub-regions, or 'hotspots' for mortality in Puget Sound, and assess interactions between body size and wild or hatchery origin, in the context of interannual variation.

METHODS

Fish collection and tagging

Natural-origin (hereafter 'wild', but with no assumptions regarding their genetic background) steelhead smolts were collected from 3 Hood Canal rivers (Big Beef Creek, Dewatto River, and South Fork Skokomish River), 2 rivers in central Puget Sound (Puyallup and Green rivers), the Nisqually River in south Puget Sound, and the Skagit River in north Puget Sound (Fig. 1) during the smolt migration periods (April–June) of 2006 through 2009. Hatchery steelhead smolts were obtained from rearing facilities associated with the Duckabush River (Lilliwaup Hatchery), the Green River (Soos Creek Hatchery), the Hamma Hamma River (Lilliwaup Hatchery), the Puyallup River (White River Hatchery), the Skokomish River (McKernan Hatchery), and the Skagit River (Marblemount Hatchery) (Fig. 1). Hatchery smolts from the Duckabush, Hamma Hamma, and

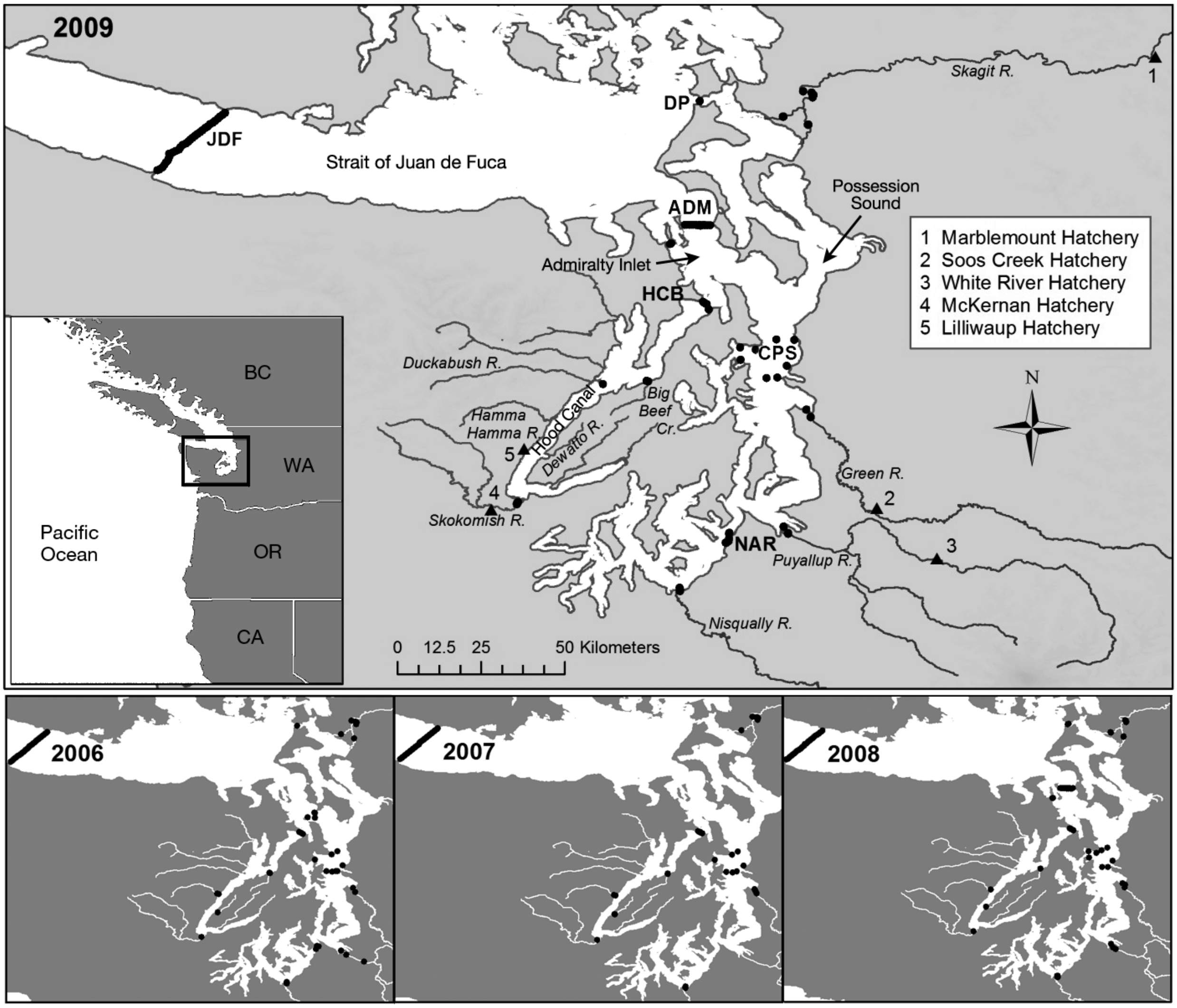

Fig. 1. Map of Puget Sound showing the locations of receiver arrays (circles) at the Hood Canal Bridge (HCB), in central Puget Sound (CPS), and in the Strait of Juan de Fuca (JDF) during all study years (2006–2009). Arrays were also deployed at Admiralty Inlet (ADM) in 2008 and 2009, at Deception Pass (DP) in 2006, 2008 and 2009 and at the Tacoma Narrows (NAR) in 2006 and 2009. One or more receivers were deployed at river mouths to determine time of saltwater entry. Triangles denote locations of hatcheries

Skokomish rivers, and the Puyallup River (2008 and 2009 smolts), were raised from natural-origin local broodstock, whereas hatchery smolts from the Green and Skagit rivers, and Puyallup River (2006 smolts), originated from a multi-generation, non-native broodstock (Chambers Creek). A total of 771 wild and 616 hatchery smolts were surgically implanted with either a V7-2L-R64K (7 × 17.5 mm [diameter × length], 1.4 g), V7-4L-R64K (7 × 18.5 mm, 1.6 g) or V9-2L-R64K (9 × 20 mm, 3.5 g) 69 kHz acoustic transmitter (VEMCO) (Table 1). Tagging occurred at the smolt collection sites and hatcheries-of-origin. Each smolt was anesthetized using MS-222 prior to surgery, and supplied with anesthetic throughout the procedure. Incisions were made anterior to the pelvic girdle, the transmitter was placed within the body cavity, and the opening was closed using 2 or 3 interrupted stitches using monofilament sutures. Smolts were held for variable time periods ranging from 1 h to 30 d before release into their respective streams (Table 1).

Receiver arrays

VEMCO VR2 receivers were deployed at each river mouth to detect tagged smolts entering seawater, and 6 main receiver 'lines' of VR2 and VR3 receivers were deployed across-channel in Puget Sound and the Strait of Juan de Fuca to detect smolts along their early marine migration (Fig. 1). During the 2006–2009

Table 1. Number of individual steelhead smolts tagged with V7 and V9 transmitters between 2006–2009, and average length, weight and release site for each tagged population. W = wild, and H = hatchery populations. rkm: river kilometer

Population	Origin	2006	2007	2008	2009	Total	Average length (mm)	Average weight (g)	Release site (rkm)
Big Beef Creek	W	37 (V9)	26 (V7)	27 (V7)	32 (V7)	122	182 ± 2	56 ± 2	0.1
Dewatto River	W		40 (V7)			40	175 ± 3	53 ± 3	0.3
Duckabush River	H				30 (V7)	30	211 ± 2	92 ± 3	1.9
Green River	W	50 (V7)	40 (V7)	48 (V7)	50 (V7)	188	185 ± 1	60 ± 1	55
Green River	H	50 (V7)	49 (V7)	50 (V7)		149	192 ± 1	66 ± 1	54.5
Hamma Hamma River	H	33 (V9)	47 (V7)			80	188 ± 2	45 ± 2	2.0
Nisqually River	W	19 (V7)	35 (V7)	3 (V7)	34 (V7)	188	198 ± 2	81.1 ± 3	0–21.2
		37 (V9)	14 (V9)	11 (V9)	35 (V9)				
Puyallup River	W	25 (V7)				25	198 ± 5	77 ± 3	17.0
	H	25 (V7)		90 (V7)	66 (V7)	181	190.1 ± 1.1	72.6 ± 1.1	55.8
Skokomish River	W	27 (V9)	51 (V7)	41 (V7)	23 (V7)	142	182.5 ± 1.6	56.7 ± 1.8	13.5
	H			42 (V7)	29 (V7)	71	187.6 ± 2.8	67.2 ± 3.4	13.5
Skagit River	W	23 (V7)	47 (V7)	50 (V7)	25 (V7)	145	170.0 ± 1.2	52.1 ± 1.1	10.0
	H			50 (V7)	55 (V9)	105	178.1 ± 1.2	62.7 ± 1.4	102
Total		326	349	412	379	1466			

smolt outmigration periods, receiver arrays spanned central Puget Sound (CPS; 7–8 receivers), northern Hood Canal at the Hood Canal Bridge (HCB; 4–7 receivers), and the Strait of Juan de Fuca (JDF; 31 receivers). In 2006, 4 receivers were deployed in southern Admiralty Inlet (too far south to detect Hood Canal populations). In 2008 and 2009, a 13-receiver line was deployed across northern Admiralty Inlet intersecting the migration path of both Puget Sound and Hood Canal populations (ADM). Two receivers covered Deception Pass (DP) in 2006, 2008, and 2009, and a group of receivers was also deployed in southern Puget Sound near the Tacoma Narrows Bridge (NAR) in 2006 (3 receivers) and in 2009 (10 receivers) (Fig. 1).

Survival and detection probability estimation

Cormack-Jolly-Seber (CJS) statistical models (Lebreton et al. 1992) were created and compared in 2 separate analyses of the smolt detection data. One set of models was constructed to estimate the probability of survival (φ) of both hatchery and wild smolts through multiple migration segments, and the detection probability (p) at each receiver line, and to evaluate possible geographic and population effects on segment-specific φ and p ('multi-segment analysis'). A second '2-segment' analysis compared models that broke the migration into only 2 segments (freshwater and saltwater), and used data from wild smolts only to identify factors affecting survival over the broader Puget Sound migration. The multi-segment analysis allowed for estimation of hatchery and wild smolt survival at a fine scale (i.e. segment-specific survival probabilities), while the 2-segment analysis focused on the entire early marine migration of wild smolts exclusively.

Models for φ and p were constructed using the RMark package (Laake & Rexstad 2007) in R (R Development Core Team 2007) for the program MARK (White & Burnham 1999). Models in the multi-segment analysis incorporated data from all 1466 tagged individuals, and models in the 2-segment analysis used data from a subset of those (850 wild smolts). Goodness-of-fit of the detection data to the global CJS model for each analysis was tested using the median $\hat{c}$ method (within MARK) and the variance inflation factors were found to be satisfactory ($\hat{c} < 2$). The CJS model cannot distinguish between mortality and emigration, so in this study, $1 - \varphi$ represents both animals that died and those that did not migrate. This issue generally tends to cause underestimation of survival, and may specifically influence freshwater survival rates of hatchery smolts as some delay migration or remain indefinitely in freshwater after release (see Hausch & Melnychuk 2012). However, all evidence indicates that once steelhead smolts enter Puget Sound they migrate to the ocean rather than remaining in Puget Sound, as some Pacific salmon species do.

Several combinations of factors and covariates were used to construct a series of models to be tested in RMark. Akaike's Information Criteria (AIC) were used to identify the set of variables that parsimoniously explained the variation in the survival and detection data (Burnham & Anderson 2010). Modeling results were adjusted using the estimated variance inflation factor ($\hat{c}$) to compute $QAIC_c$ values, which are adjusted AIC values that compensate for

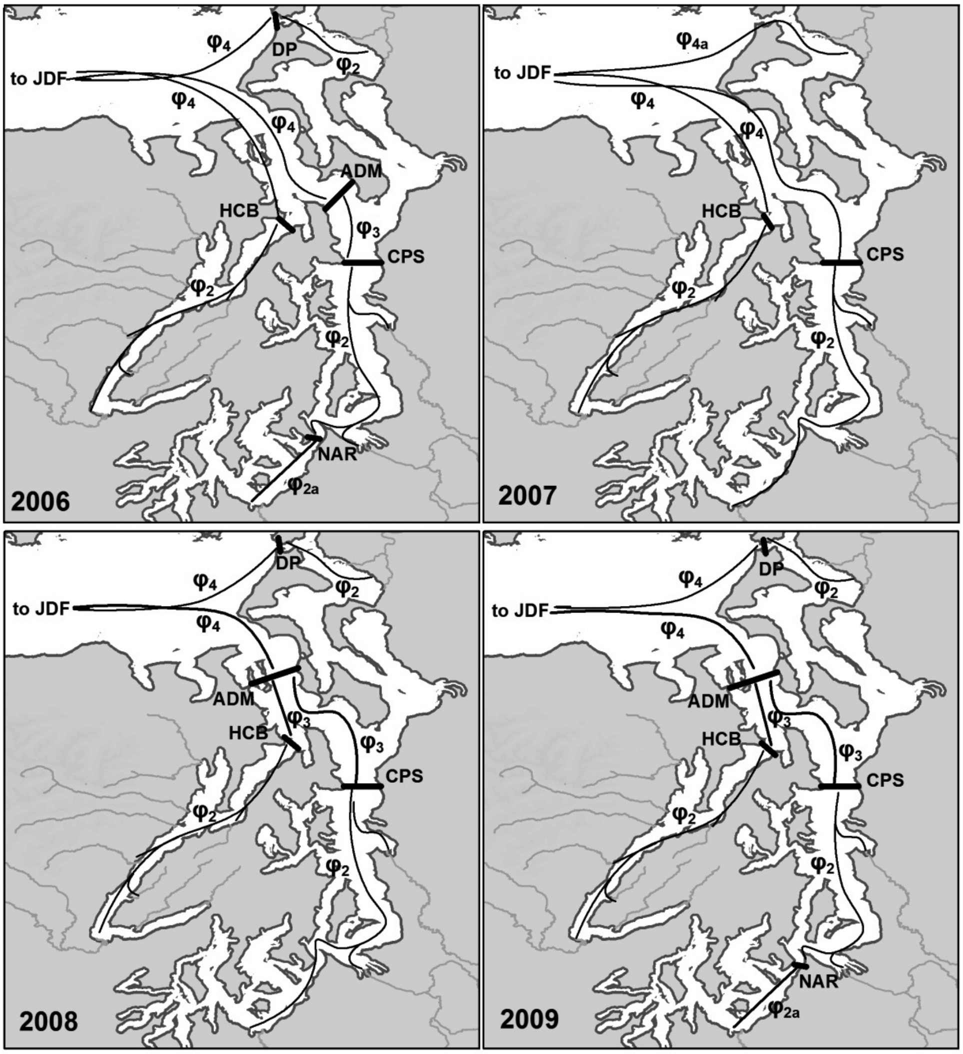

Fig. 2. Migration segments for which survival probability was estimated by year, defined by annual variation in receiver array locations. φ_1 = segment from point of release (PR) to river mouth (RM), φ_2 = RM to either the Hood Canal Bridge (HCB; Hood Canal Rivers), the Central Puget Sound line (CPS; Nisqually, Puyallup, and Green River smolts), or the Deception Pass line (DP; Skagit River smolts) segments, φ_{2a} = RM to Narrows Bridge (NAR; 2006 and 2009 only) segment, φ_3 = HCB/CPS to the Admiralty Inlet line segment (ADM; no Skagit), φ_4 = the ADM or DP to the Strait of Juan de Fuca line (JDF) segment, and φ_{4a} = RM to JDF (Skagit only) segment. See 'Materials and Methods: Survival and detection probability estimation' for additional explanation

extra-binomial variation. The model with the lowest $QAIC_c$ was considered the best fit, given the detection data, though models with $\Delta QAIC_c < 2$ were also considered to have substantial support. Models with $\Delta QAIC_c > 4$ have considerably less support, and a $\Delta QAIC_c > 10$ suggests a failure of the associated model to explain substantial variation (Burnham & Anderson 2010). A 95% confidence set of models was compiled for each of the 2 mark-recapture analyses by adding up the model Akaike weights from largest to smallest until the sum exceeded 0.95. Estimates of the relative importance of predictor variables were calculated by summing the Akaike weights across all models in the confidence set where that variable was included (Burnham & Anderson 2010).

In the multi-segment analysis, detection data for each smolt at each receiver line were used to construct individual encounter histories, which allowed estimation of φ and p through either 4 migration segments (Hood Canal, Nisqually, Puyallup and Green River smolts) or 3 migration segments (Skagit River smolts): φ_1 = point of release (PR) to river mouth (RM), φ_2 = RM to either the HCB (Hood Canal Rivers), CPS (Nisqually, Puyallup, and Green River smolts), or DP (Skagit River smolts), φ_3 = HCB/CPS to the ADM (no Skagit), φ_{4a} = RM to JDF (Skagit only), or φ_4 = ADM to JDF (Fig. 2). In 2008, 5 Skagit River smolts migrated south through Possession Sound and were detected at the ADM line; these detections were combined with the DP detections to calculate one estimate of φ and p. During years when receiver lines were absent (ADM in 2006 for Hood Canal smolts and 2007 for all smolts, and DP in 2007 for the Skagit smolts), the 2 migration segments using that line became one (Fig. 2). A separate CJS model was set up to estimate φ for Nisqually smolts during the years when receivers were deployed near the Narrows Bridge to get a survival probability estimate for RM to NAR

(φ_{2a}) for years 2006 and 2009 (Fig. 2). Including data from the NAR line in the larger CJS model would have resulted in a mismatch of comparisons between migration segments and was not available for all years.

The survival probability portion of the multi-segment models included linear and multiplicative effects of the following factors alone and in combination: 'migration segment', 'year', 'release date' (levels = late April [16–30 April], early May [1–15 May], late May [16–31 May], or early June [1–15 June]), 'population', 'rear type' (i.e. hatchery or wild), or a 'rear type:population' variable that represented each rear type × population combination (e.g. Skokomish Hatchery, Skokomish Wild, Nisqually Wild, etc.). A 'region' factor was substituted for 'population' in a set of models to determine whether survival of geographically similar populations covaried. Regions were defined as Hood Canal (Big Beef Creek, Dewatto, Hamma Hamma, and Skokomish rivers), Central and South Sound (Green, Puyallup, Nisqually rivers), and North Sound (Skagit River). The detection probability portion of the multi-segment models was parameterized to produce separate estimates of p for each river mouth and for each receiver line. A 'year' factor was included in all candidate models since receiver lines were often redeployed each year. A 'tag type' factor was also included in each detection model to estimate different p for V7 and V9 tagged smolts.

The 2-segment models used detections from river mouth receivers and the JDF line to create a condensed encounter history for each wild steelhead smolt. Models were constructed to estimate smolt survival from PR to RM, and from RM to JDF only. The main purpose of this second analysis was to examine how wild Puget Sound survival rates were affected by smolt size (fork length) and release date, 2 factors hypothesized to work over a longer migration distance to affect overall survival through Puget Sound. As we sought broad rather than isolated or variable effects in the 2-segment analysis, candidate models included only additive effects of 'year'. Interactions between 'segment' and 'release date', and 'segment' and 'fork length' were modeled because we were interested in possible differences in the effects of release date and body size in freshwater and marine portions of the route. Terms for the linear and interaction effects of 'population' were also included in some candidate models to examine possible effects of geography. The detection portion of these 2-segment models included the same parameters ('year' and 'tag type') as the multi-segment models.

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 line. To circumvent this problem, empirically derived estimates from similarly sited and configured receiver lines were used to fix p at the JDF line (Melnychuk 2009). Melnychuk (2009) calculated mean and 95% confidence limit estimates of p for V7 and V9 VEMCO tags passing a receiver line spanning the Strait of Georgia in 2004, 2005, 2006, and 2007, so we used an average of the 2005–2007 values (2004 was an anomalous year) for all years to fix the value of p for the JDF line in our models ($p_{JDF(V7)}$ = 0.685, $p_{JDF(V9)}$ = 0.909). An empirical estimate of the JDF line was also calculated for V7 tags by comparing detections of V9H ('high power') and V7 tags in spring 2014. Equal numbers of V9H and V7 tags were surgically implanted in Skagit River hatchery smolts, treated identically, and released at the same time into the Skagit River. In 2013 studies of Skagit hatchery smolts, each V9H tag at the JDF line was detected an average of 216 times, and always on at least 2 receivers, indicating 100% detection of those tags. In 2014, 6 out of 50 V9H tags were detected at JDF an average of 48 times, always on at least 2 receivers, compared to only 4 out of 50 V7 tags detected (E. J. C. unpubl. data). The relative rate of detection for V7 tags was therefore calculated as 66.67%, a rate very similar to the mathematically derived estimate of 68.5%.

Survival curves were constructed for each population using survival probabilities derived from the segment-specific survival model in the 95% candidate set that defined the most variation in segment survival estimates (φ(segment + rear type:population + year), $\Delta QAIC_c$ = 2.761; Table 2). Survival through each migration segment was compared between populations by distance-based instantaneous mortality rates:

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

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

Migration behavior

Travel rates and travel times were calculated for all marine segments to examine migratory behavior. Travel time was calculated as the time in days between the last detection at the first detection line in the migration segment and the first detection at

Table 2. Confidence set for the multi-segment mark-recapture analysis, which tested effects of population, rearing type, population, region, and year on survival of steelhead smolts through 3 or 4 migration segments (depending on population). All survival portions of the model are paired with a receiver line, tag type, and year-specific detection probability portion (p(line + tagtype + year))

Model	$QAIC_c$	$\Delta QAIC_c$	Weight
φ(segment + rear type × population + year)	2590.389	0.000	0.433
φ(segment + rear type × population + release date + year)	2591.889	1.500	0.205
φ(segment × rear type × population + year)	2593.15	2.761	0.109
φ(segment × release date + rear type × population + year)	2594.719	4.330	0.050
φ(segment × rear type + population + year)	2594.968	4.579	0.044
φ(segment × population + rear type + year)	2595.635	5.246	0.031
φ(segment + rear type + population + year)	2595.963	5.574	0.027
φ(segment + population × rear type)	2596.006	5.617	0.026
φ(segment × rear type × region + release date + year)	2598.287	7.898	0.008
φ(segment × population + release date + rear type + year)	2598.603	8.214	0.007
φ(segment × rear type + year + region)	2598.617	8.228	0.007
φ(segment + release date + rear type × population)	2598.753	8.364	0.007

the subsequent detection array. Travel rate was the straight line in-water distance (km) between segment detection arrays divided by the travel time. Segments were categorized as either initial marine ('initial') (RM to HCB/DP/CPS), Admiralty Inlet (ADM) (HCB/CPS to ADM), or Strait of Juan de Fuca (JDF) (ADM/DP to JDF). Travel rates were log transformed to achieve normality. Analysis of covariance was used to test for effects of region (Hood Canal, Central and South Sound, or North Sound) and rearing type on initial and ADM travel rate ([log]travel rate ~ region + region:rear type + fork length), and to test for differences in travel rate by segment ([log]travel rate ~ segment + fork length; all regions pooled). Factors were considered significant at the 0.05 level and the Tukey's HSD method was used to compare levels of region and segment. The data were not sufficient to analyze the effect of rearing type on JDF travel rate, so only the effect of region was tested ([log]travel rate ~ region + fork length).

RESULTS

Survival

Marine survival probabilities (RM to JDF) ranged from 0.8% (Skokomish hatchery population in 2009) to 39.3% (Big Beef Creek wild population in 2006), and averaged 16.0% for wild smolts and 11.4% for hatchery smolts over the 4 years of the study. RM to JDF survival was generally highest in 2006, similar between 2007 and 2008, and lower in 2009. Freshwater survival probabilities were high relative to early marine estimates, ranging from 63.6% (Skokomish Hatchery population, 2009) to 94.9% (Big Beef Creek in 2006), though, for most populations, distances between PR and RM distances were much shorter than RM to JDF distances (Table 1, Fig. 1).

The survival portion of the multi-segment model with the lowest $QAIC_c$ (φ(segment + rear type:population + year)) estimated separate survival probabilities for each population × rear type combination through each migration segment, and adjusted those probabilities with an additive year effect (Table 2). The population × rear type interaction indicated that the relationship between hatchery and wild smolt survival varied by river. That is, hatchery smolt survival was lower than wild smolt survival in some populations but not others. In general, Skagit, Hamma Hamma, and Duckabush river hatchery smolts had higher estimated survival probabilities than Green, Skokomish, and Puyallup river hatchery smolts (Fig. 3). The rear type factor was present in every model in the 95% confidence set, giving that variable the highest relative weight possible (1.0). Population and year were also important variables in estimating survival of steelhead smolts, with weights >0.965 (Table 3). Regional patterns of survival were not supported by the data ($weight_{region}$ = 0.009); the model with the lowest AIC_c that included the region variable had a fairly high ΔAIC_c value (8.228) (Table 2). Release date effects were less important than rear type, population, and year effects in the multi-segment analysis ($weight_{release\ date}$ = 0.281) (Table 3).

Release date was associated with survival in the 2-segment analysis. The top model simply estimated a separate survival rate for each release date (φ (segment + release date)) (Table 4), leaving out effects of both population and year. The second

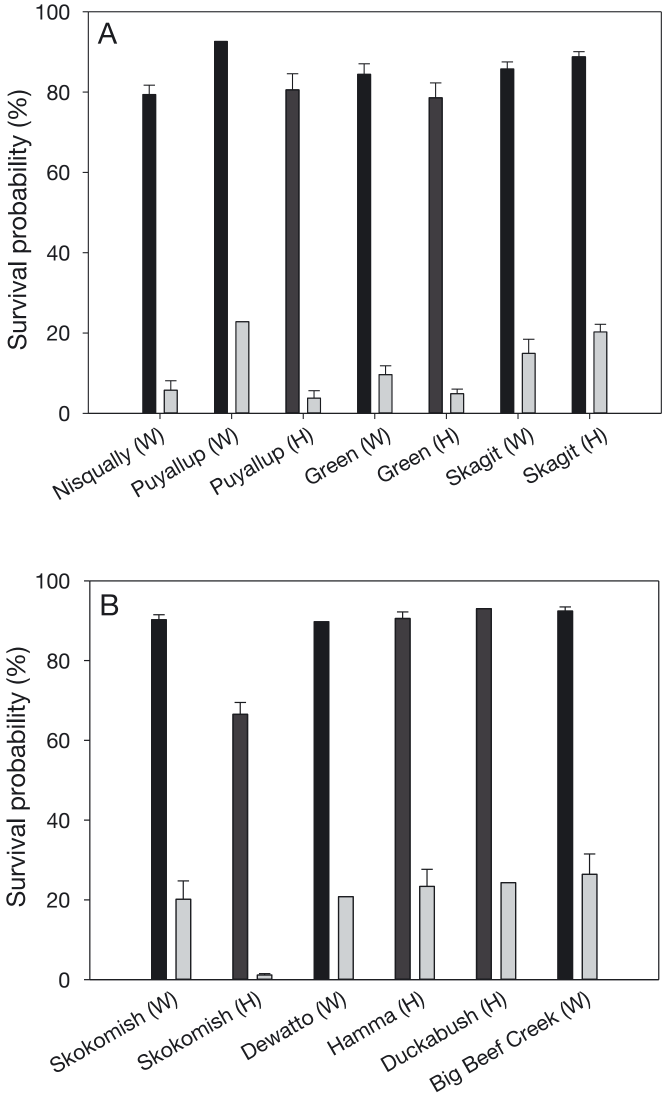

Fig. 3. Average freshwater and early marine survival probabilities ± SE for (A) all Hood Canal and (B) Puget Sound wild (W) and hatchery (H) tagged steelhead populations. Black bars = freshwater stage (point of release to river mouth), grey bars = early marine stage (river mouth to the Strait of Juan de Fuca line)

best model, however, had a negligible $\Delta QAIC_c$ (0.815) and included both a size and a year effect (φ (segment + release date + fork length + year)) (Table 4). Both models indicated substantial variation in freshwater and marine survival probabilities, and considerable variation in survival by release date in all populations in all years. The probability of survival was lowest for fish released in early May and highest in late April (Fig. 4). Though fork length was included in the second most parsimonious model, relative weight analysis did not provide evidence of substantial size selective mortality in rivers or in Puget Sound ($weight_{fork\ length} = 0.299$) (Table 5).

Table 3. Relative importance (sum of Akaike weights of models in the 95% confidence set containing each variable) of each variable tested in the multi-segment mark-recapture analysis of steelhead smolt survival

Model variable	Weight
Rearing type (hatchery or wild)	1.00
Population	0.984
Year	0.966
Release date	0.281
Region	0.009

Table 4. Confidence set for the 2-segment mark-recapture analysis, which tested the effects of population, release date, body size (fork length), and year on freshwater (point of release to river mouth) and Puget Sound (river mouth to the Strait of Juan de Fuca line) wild steelhead smolt survival using the same model for *p* (*p*(line + tagtype + year + distance))

Model	$QAIC_c$	$\Delta QAIC_c$	Weight
φ(segment + release date)	838.709	0.000	0.347
φ(segment + release date + fork length + year)	839.5243	0.815	0.231
φ(segment + release date + year)	839.9426	1.234	0.187
φ(segment + year)	844.0033	5.294	0.025
φ(segment × release date + fork length)	844.1769	5.468	0.023
φ(segment × fork length + release date + year)	844.1841	5.475	0.022
φ(segment × release date)	844.5654	5.856	0.019
φ(segment + population + release date)	844.856	6.147	0.016
φ(segment × release date + fork length + year)	844.8575	6.149	0.016
φ(segment × fork length + release date)	844.901	6.192	0.016
φ(segment + fork length + year)	844.9576	6.249	0.015
φ(segment × release date + year)	845.4483	6.739	0.012
φ(segment)	845.4484	6.739	0.012
φ(segment × population + release date)	845.6098	6.901	0.011

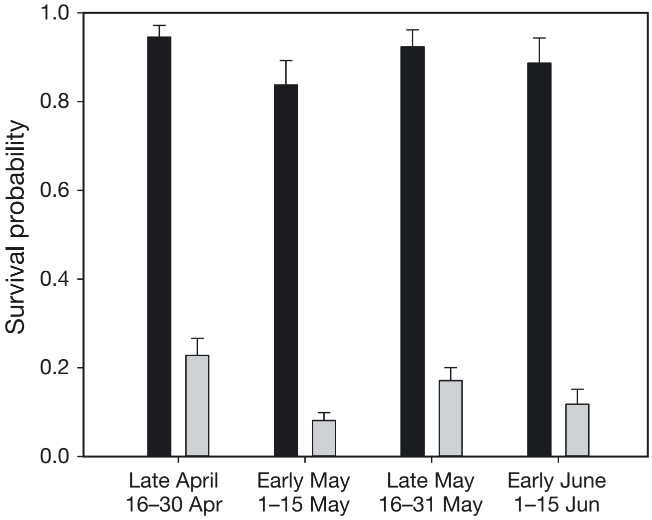

Fig. 4. Freshwater and early marine survival probability estimates ± SE by release date, derived from the top 2-segment model (φ (segment + release date + year)). Black bars = freshwater stage (point of release to river mouth), grey bars = early marine stage (river mouth to the Strait of Juan de Fuca line)

Table 5. Relative importance (sum of Akaike weights of models in the 95 % confidence set containing each variable) of each variable tested in the 2-segment mark-recapture analysis to explain the survival of steelhead smolts

Model variable	Weight
Release date (factor)	0.946
Year	0.534
Body size (fork length)	0.299
Population	0.028

The highest distance-based instantaneous mortality rates were estimated for Big Beef Creek smolts from HCB to ADM during 2008 (4.8 % mortality per km) and 2009 (5.5 % mortality per km), (Fig. 5). Other relatively high mortality rates were estimated for smolts migrating from the Green River to the CPS in all study years (range = 3.2–4.4 % mortality per km), for Skokomish River smolts through HCB to ADM in 2008 (1.7 % mortality per km) and 2009 (2.0 % mortality per km), and for Nisqually River smolts through

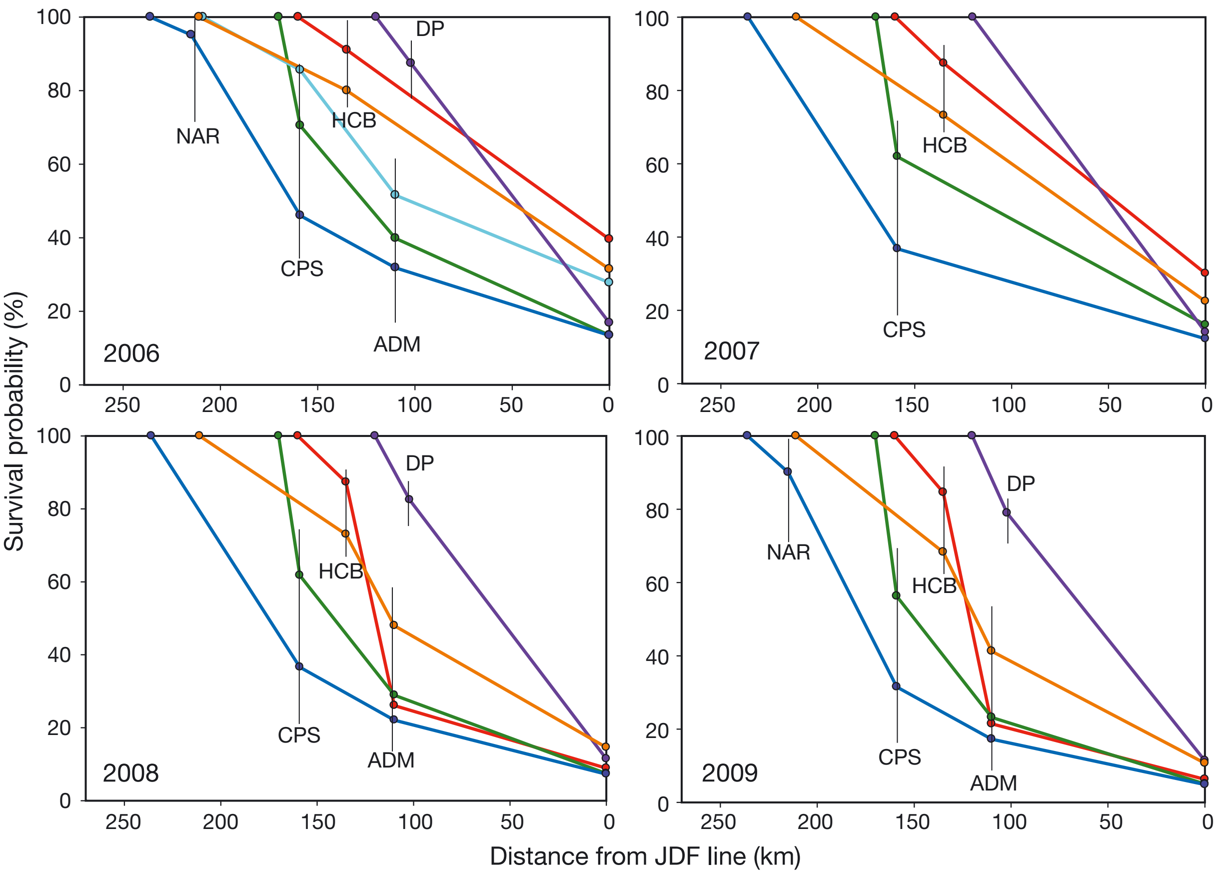

Fig. 5. Estimated survival probabilities for steelhead plotted at each receiver array along the marine migration pathway for years 2006 to 2009. Survival estimates are shown for only wild smolts from Big Beef Creek (red), Green River (green), Nisqually River (dark blue), Skagit River (purple), Skokomish River (orange), and the Puyallup River (light blue)

RM to CPS in 2008 (1.0% mortality per km) and NAR to CPS in 2009 (0.9% mortality per km).

Migratory behavior

Steelhead smolts migrated quickly through Hood Canal and Puget Sound. Average population-specific travel times from RM to the next marine line ranged from an average of 1.8 d for hatchery and wild Green River smolts (RM to CPS; 11 km) to 12.8 d for the Skokomish River smolts (RM to HCB; 75 km) (Table 6). Average RM to ADM travel time ranged from 5.7 d for hatchery and wild Green River smolts (47 km) to 13.2 d for hatchery and wild Puyallup River smolts (86 km) (Table 6). Green River smolts exhibited the shortest population-specific travel times (6.2 d) over the entire early marine migration (RM to JDF; 157 km). The longest average travel time was 18.1 d (Skokomish River smolts, 210 km).

Travel rates differed significantly by migration segment (F = 28.93, p < 0.001) (Fig. 6). Smolts traveled significantly slower through initial marine migration segments in Puget Sound and Hood Canal ($\bar{x}$ = 12.04 km d^{-1}) than through Admiralty Inlet ($\bar{x}$ = 21.50 km d^{-1}) (Tukey's HSD, p < 0.001). Travel rates through the Strait of Juan de Fuca ($\bar{x}$ = 34.14 km d^{-1}) were significantly faster than Admiralty Inlet travel rates (Tukey's HSD, p < 0.001), indicating increasing travel rates as smolts neared the Pacific Ocean.

Initial marine travel rates differed by region (F = 16.75, p < 0.001). Hood Canal smolts travelled more slowly ($\bar{x}$ = 10.11 km d^{-1}) than south and central Puget Sound smolts ($\bar{x}$ = 15.22 km d^{-1}) (p < 0.001), but not significantly more slowly than Skagit smolts ($\bar{x}$ = 15.20 km d^{-1}, p = 0.360). South and central Puget Sound smolts and Skagit smolts did not travel at significantly different rates through the initial marine segment (p = 0.401) (Fig. 6A). Hatchery and wild smolt initial marine travel rates did not differ (p = 0.440). Fork length had a slight effect on initial marine travel rate, with larger smolts travelling faster than smaller smolts (F = 4.88, p = 0.027). Neither Admiralty

Table 6. Average travel time (d ± SE) for all populations through cumulative migration segments for all 4 years of the study (2006–2009). Hatchery and wild smolt travel times are pooled. na = not applicable

Population	RM to CPS	RM to DP	RM to HCB	RM to ADM	RM to JDF
Nisqually	5.7 ± 0.6	na	na	8.8 ± 1.1	12.2 ± 0.7
Puyallup	5.9 ± 0.8	na	na	13.2 ± 1.2	10.3 ± 0.4
Green	1.8 ± 0.3	na	na	5.7 ± 0.8	6.2 ± 0.5
Skagit	na	2.9 ± 0.4	na	na	7.2 ± 1.0
Skokomish	na	na	12.8 ± 1.4	12.2 ± 1.9	18.1 ± 1.5
Dewatto	na	na	12.4 ± 1.5	na	16.0 ± 1.8
Hamma	na	na	9.8 ± 1.6	na	11.3 ± 1.2
Big Beef	na	na	6.5 ± 0.6	6.1 ± 1.9	15.0 ± 1.4

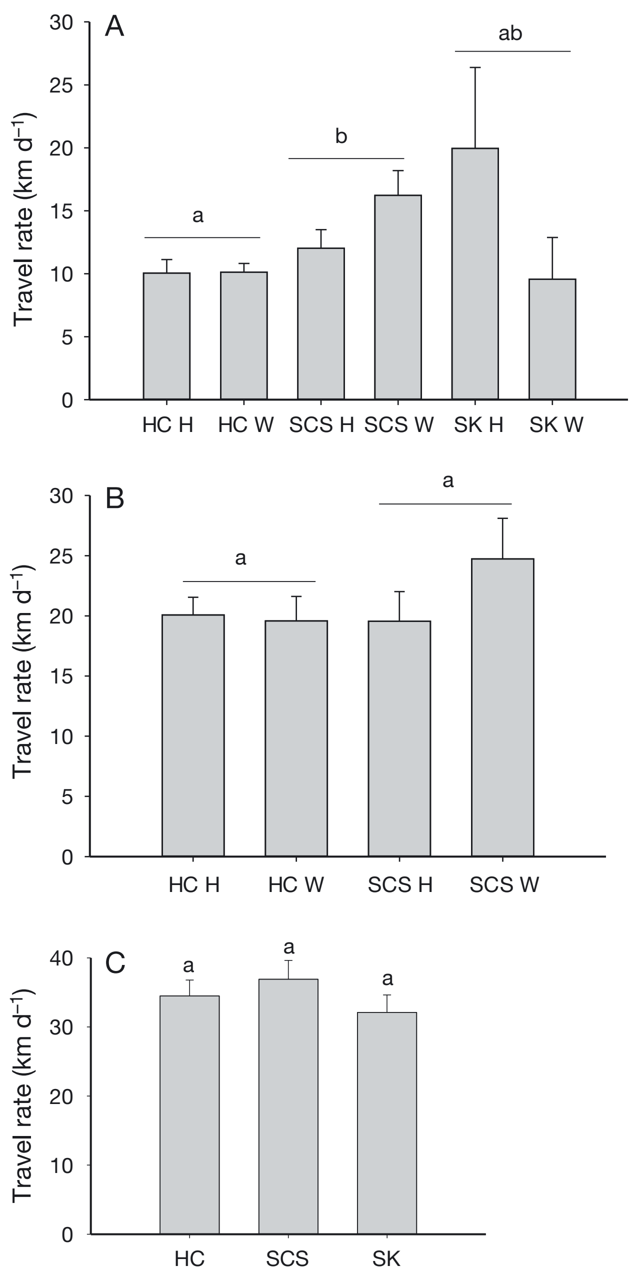

Fig. 6. Comparison of average (± SE) steelhead smolt travel rates for hatchery (H) and wild (W) smolts from either the Hood Canal (HC), South and Central Sound (SCS), or Skagit (SK), through (A) the initial marine segment, (B) Admiralty Inlet, and (C) Strait of Juan de Fuca. Different letters denote statistically significance differences (α = 0.05)

Inlet nor JDF travel rates differed by region or rear type (all $p > 0.258$) (Figs. 6B,C), and were not affected by fork length ($F = 0.468$, $p = 0.628$, and $F = 0.842$, $p = 0.481$ for ADM and JDF, respectively).

DISCUSSION

The high mortality estimated for steelhead smolts migrating through Puget Sound is consistent with estimates of low overall marine survival of these populations over the past several decades. Our analysis of Puget Sound populations indicated that only about 16% of wild and 11% of hatchery smolts that left the mouths of their natal rivers survived to reach the Pacific Ocean. Previous analyses indicated similar early marine survival rates for steelhead migrating to sea from the Strait of Georgia, British Columbia (Melnychuk et al. 2007, Welch et al. 2011). Low survival rates have been reported widely for steelhead and other salmonids entering various coastal habitats, especially estuaries. Halfyard et al. (2012) recently found that migrating Atlantic salmon smolts survived at low rates through estuaries in relation to freshwater and bay habitats in a Nova Scotia river system. In the Alsea River, Oregon, 78% of wild steelhead smolts survived a 74 km downstream migration, followed by 60% survival in only 9 km of estuary habitat (Johnson et al. 2010). Chinook salmon *Oncorhynchus tshawytscha* and steelhead smolts sustained low mortality rates in the upper Columbia River estuary (0.1% mortality per km), but died at a much higher rate (1.2% mortality per km) when they neared the river mouth (Harnish et al. 2012). A study conducted on the Napa River in California contradicts the low early marine survival pattern documented in several coastal environments; 85% of steelhead smolts survived through the estuary and San Francisco Bay (~ 42 km), and continued to experience high survival (at least 60%) after traveling 58 km along the California coast (Sandstrom et al. 2013). Finer scale research into the mechanisms of early marine mortality may explain why some geographic locations promote more successful migration to the open ocean than others.

Survival probabilities varied substantially by migration segment, though patterns were not always consistent among populations. Green and Skagit river smolts experienced their highest mortality rates in the initial marine segment (RM to CPS and RM to DP, respectively), which is similar to other steelhead studies documenting relatively high mortality upon saltwater entry (Johnson et al. 2010, Clements et al. 2012). Melnychuk et al. (2013) found that coho salmon and steelhead smolt mortality was greater within 5 km of the Squamish River mouth than anywhere else in Howe Sound, British Columbia. In contrast, Hood Canal populations generally survived better through the initial marine segment, and subsequently experienced high mortality in a short distance over the second marine survival segment from the Hood Canal Bridge through Admiralty Inlet. A substantial portion of the HCB to ADM mortality may be associated with the Hood Canal Bridge itself. Detailed behavioral analysis suggests that the Hood Canal Bridge causes migration delays and abnormal movement patterns that may increase predation on steelhead smolts in the vicinity (Moore et al. 2013). Although steelhead smolt populations typically experience their highest mortality rates during their initial marine migration segment, habitat-specific conditions can contribute substantially to variation in mortality rates among regions.

The broader ('2-segment') mark-recapture analysis identified release date as an important factor explaining variation in freshwater and saltwater survival. Smolts released in early May, regardless of population of origin, experienced very low RM to JDF survival each year of the study (see Fig. 4). Natural processes such as harmful algal blooms or disease outbreaks would seem unlikely to contribute to extra mortality during a specific time period on an interannual basis. A predator response to the consistently timed release of hatchery steelhead in early May could explain the increased mortality. Approximately 70–95% of all 1–2 million hatchery steelhead smolts released into Puget Sound were released during the first week of May, and 1.9–2.6 million coho smolts were released in very late April/early May during the 2006–2009 study period (K. Henderson unpubl. data), coinciding with the lowest smolt survival rates. Predators respond to large releases of hatchery salmon by increasing local density, i.e. an aggregative response (Wood 1985, Collis et al. 1995), which may increase consumption of otherwise less densely congregated wild conspecifics. Higher survival rates observed before and after major hatchery releases may be attributed to low smolt densities that escape the attention of opportunistic predators. Steelhead migrating with large groups of hatchery fish could be more vulnerable if predators have the capacity to consume large numbers of smolts.

Though release date was an important factor in the 2-segment analysis, it did not substantially explain variation in survival patterns in the multi-segment analysis. The difference in the outcomes of the 2 analyses stems from the inclusion of hatchery smolts in the multi-segment analysis. The hatchery smolts used in this study were released within a short window of time, while wild smolt release dates were more variable throughout the outmigration period. For example, hatchery smolts from the Soos Creek hatchery (Green River) and the Marblemount hatchery (Skagit River) were all released on one day. There were few early- and late-released smolts within the hatchery groups with which to test the effect of release date, and release date was closely associated with population, which was an important factor in the multi-segment analysis. If there had been more variation in release timing of hatchery smolts, the effect of release date may have been stronger in the multi-segment analysis.

Fork length was not a significant predictor of survival probability, so early marine survival in Puget Sound seems to be somewhat indiscriminant of body size. However, analysis of Skagit River steelhead scales indicated size selective smolt-to-adult survival (Thompson & Beauchamp 2014), and smolt size was positively correlated with adult survival of both Columbia River (Evans et al. 2014) and Keogh River steelhead (Ward et al. 1989). Size selective mortality has been observed in other species of salmon as well; adults that had been large as smolts were over-represented, relative to the abundance of that size class, among the smolts (Healey 1982, Holtby et al. 1990, Henderson & Cass 1991). Our study focused only on survival within Puget Sound rather than on survival over the entire (smolt-to-adult) marine period, so body size may play a larger role in survival patterns once smolts enter the Pacific Ocean. The time scale over which the process of size selectivity was measured was also short since steelhead spend little time in nearshore habitats, and patterns may take longer to resolve. In a telemetry study of early marine survival of British Columbian coho, Chinook, steelhead, or sockeye salmon, Welch et al. (2011) found no evidence of a difference in size between released smolts and those determined to be survivors. Halfyard et al. (2013) demonstrated that the shape and direction of the body size to survival relationship can change with watershed and habitat type. Ward (2000) reported size selective mortality of Keogh River (British Columbia) steelhead for several years up to the year 1990, when population abundance began to decline, suggesting that density-dependent factors affect size selective mortality. Size-selective mortality of Puget Sound steelhead was not evident during the migration to the open ocean in the present study, but may operate at a later life history stage, over a different time scale, or during periods of higher population abundance.

Rearing history accounted for substantial variation in smolt survival across multiple migration segments. Hatchery-smolt survival probabilities were generally less than for wild smolts, though smolts from some hatchery populations had comparable or better survival than wild smolts in some migration segments. The higher survival of Skagit, Duckabush, and Hamma Hamma River hatchery smolts in relation to survival of Skokomish, Green, and Puyallup River hatchery smolts cannot be explained by differences in broodstock type (locally derived, natural origin, vs non-local multi-generation). For example, Skagit River smolts (Chambers Creek broodstock) survived at higher probabilities than most wild populations in this study, and local wild broodstock hatchery smolts from the Skokomish and Puyallup. Skagit River smolts were smaller and Duckabush smolts larger than average, so body size does not appear to explain differences among hatcheries. Rearing practices and hatchery conditions (i.e. rearing density, feeding frequency) probably influenced survival differences between Skokomish River wild and hatchery smolts, and between Skokomish and Duckabush River hatchery smolts (Moore et al. 2012), and are likely to have played a role in the current expanded study as well.

Steelhead smolts travelled quickly through the estuary and Puget Sound. Nisqually River smolts travelled the longest distance from their river mouth to JDF (233 km) in as little time as 10 d (average 12.2 d). Some Pacific salmon species rear in nearshore environments extensively as juveniles (notably Chinook and chum salmon) before migrating to the ocean (Quinn 2005). A considerable fraction of the Chinook and, to a lesser extent, coho salmon, remains in Puget Sound waters to maturity without migrating to the coastal ocean. In contrast, steelhead migrate directly out of Puget Sound and offshore (Hartt & Dell 1986). Smolts originating in Hood Canal rivers travelled more slowly though Hood Canal than Nisqually, Puyallup, and Green river smolts travelled through their initial marine segment in Puget Sound. Perhaps current patterns or better foraging opportunities retained smolts in Hood Canal longer than smolts in other areas. All populations travelled through the final ADM to JDF migration segment faster than through any other measured segment, averaging about 34 km d^{-1} (approx. 2 body lengths [BL] s^{-1} for a 200 mm smolt). The range of maximum sustainable swimming speeds for similarly sized sockeye salmon is 0.8–2.0 BL s^{-1} (Hinch et al. 2006), suggesting that steelhead smolts approaching the Pacific Ocean were travelling very fast, even if aided by tidal currents.

Short residence times, coupled with the high freshwater and low Puget Sound survival probabilities observed in this study, suggest a source of mortality that acts quickly on a large number of smolts in the early marine environment. If predators are abundant, predation fits this pattern and may explain the low RM to JDF segment survival probabilities measured over less than 2 wk. Bottom-up processes (e.g. lack of suitable prey) that may cause starvation in migrating smolts are unlikely to act on such time-scales. Puget Sound Chinook salmon populations have experienced declines in recent decades, and juvenile survival has been linked to rapid growth in the early marine environment (Duffy & Beauchamp 2011). However, Chinook salmon typically spend 2–3 mo in estuaries and nearshore environments, whereas steelhead use these habitats very briefly and primarily as migration corridors. It is also unlikely that direct mortality from disease affected large numbers of smolts, as neither overt signs of distress nor external signs of disease were observed on any of the tagged steelhead from the 6 wild populations. However, it is possible that asymptomatic fish with chronic infections would demonstrate decreased swimming performance, resulting in their predisposition to capture by predators (P. Hershberger pers. comm.). Hostetter et al. (2011) found that migrating steelhead smolts with poor body condition were more likely to be prey for birds than healthy smolts in the Columbia River. Whether acting on healthy or diseased fish, predation most plausibly explains the rapid mortality rates evident in steelhead smolts migrating through Puget Sound, although the primary predators on steelhead in Puget Sound are essentially unknown.

Healthy populations of marine mammals in the Salish Sea have the potential to consume a large proportion of steelhead migrants, and may account for the high rates of mortality sustained in Puget Sound. As Puget Sound steelhead populations have declined, marine mammal populations have steadily increased. Harbor seal *Phoca vitulina* populations increased rapidly from the 1970s until just before the turn of this century (Jeffries et al. 2003), and harbor porpoise *Phocoena phocoena* have expanded distribution and increased in abundance as well. Harbor seals forage opportunistically and shift diet seasonally based on prey availability (Lance et al. 2012) and prey on steelhead smolts in some locations (Laake et al. 2002). In the Puntledge River, British Columbia, harbor seals adapted their foraging behavior to ambush migrating salmon smolts under a lighted bridge (Yurk & Trites 2000). Diet information on harbor porpoises in the Salish Sea indicates little or no predation on salmonids at any life stage, though data are temporally limited and only represent stranded animals (Walker et al. 1998, Nichol et al. 2013).

Some bird species prey on juvenile salmonids, and may target smolts exiting rivers. Columbia River predation studies found steelhead to be particularly vulnerable to birds, presumably due to their tendency to migrate near the surface of saline water bodies (Collis et al. 2001). However, tagged steelhead smolts were not eaten by birds in the Nehalem River (Oregon) estuary, where more than half of coho hatchery smolts were consumed by double crested cormorants *Phalacrocorax auritus* and Caspian terns *Hydroprogne caspia* (Clements et al. 2012). Puget Sound supports populations of several seabirds capable of consuming a 150–200 mm smolt, which include cormorants, Caspian terns, loons *Gavia* sp., common murres *Uria aalge*, but none of these species have dramatically increased in abundance since the 1980s, when steelhead populations began to decline.

The present study supports the general understanding that anadromous salmonid mortality rates during the early marine period exceed those during later periods when fish are larger and in different environments (Ricker 1976). Partitioning of marine mortality rates in nearshore and offshore environments has typically been inferred by estimating early marine mortality rates and considering them in the context of overall smolt-to-adult mortality. The limited empirical evidence suggesting higher mortality in the early marine period than in later marine periods comes from conventional marking studies, on e.g. pink salmon *Oncorhynchus gorbuscha* (Parker 1968), chum salmon *Oncorhynchus keta* (Wertheimer & Thrower 2007), and has recently been corroborated by acoustic telemetry studies that estimate mortality in inland marine waters (Welch et al. 2011, Halfyard et al. 2012). Data from this analysis suggests that wild steelhead smolts survive the migration from river mouth to the Strait of Juan de Fuca at rates between 2.4 and 39.3%. Using an instantaneous mortality rate (based on the above estimated survival rates and average population-specific travel times) we can project forward the percentage of smolts remaining after only one month at sea (range = 0–3.2%). Mortality rates after open ocean entry must decrease thereafter for there to be any adult steelhead returns. Understanding the specific mechanisms causing high early marine mortality rates of Puget Sound steelhead trout populations could be critical in predicting their viability over the long term and identifying management measures to improve the status of populations.

Summary

Comparing the similarities and differences in survival among Puget Sound steelhead populations helps resolve patterns and identify trends in steelhead migration behavior and mortality. Hood Canal populations survived with higher probability than central and south Puget Sound populations through the initial marine migration segment, but experienced high mortality per kilometer between the Hood Canal Bridge and the Admiralty Inlet line. Rearing type was the most important predictor of survival through multiple segments of Puget Sound; hatchery populations generally survived poorly but some comprised similar survival rates to wild populations. Early marine survival of wild smolts depended on release date, with low estimated survival rates coincident with large-scale hatchery releases in early May. There was also a decrease in early marine survival over the 4 year study period. Short Puget Sound residence times and high rates of mortality implicate predation as the most likely mortality mechanism acting on smolts between saltwater entry and arrival in the Pacific Ocean.

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