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Comparative migratory behavior and survival of wild and hatchery steelhead (*Oncorhynchus mykiss*) smolts in riverine, estuarine, and marine habitats of Puget Sound, Washington

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Abstract Declines in the survival of steelhead (*Oncorhynchus mykiss*) populations in protected waters of Washington and British Columbia have drawn attention to the need for more information on migratory patterns and losses in river, estuary, and nearshore habitats. Accordingly, acoustic telemetry was used to quantify movements by wild and hatchery steelhead smolts released from 2006 to 2009 in the Green River, and tracked through Puget Sound, Washington. Survival varied by release group and migration segment but overall survival rates from release to the Strait of Juan de Fuca were 9.7 % for wild and 3.6 % for hatchery fish. These rates are low relative to similar studies on steelhead. Survival was higher for wild fish along all migration segments than hatchery-origin fish; the greatest loss for both groups coincided with the slowest travel rates as fish first entered the estuary and as they exited Puget Sound. Wild fish travelled faster than hatchery fish in the river (15.1 vs. 4.4 km/d) with the fastest travel in the lower river (41 vs. 20.2 km/d) and slowest immediately after release (3.7 vs. 2.4 km/d). The travel rates of wild and hatchery fish became progressively more similar over time: 15.4 vs. 10.6 km/d in the estuary, and 10.3 vs. 9.3 km/d in nearshore areas. Movement was primarily nocturnal in the river, nearly equal between day and night in the upper estuary, and predominately diurnal in the lower estuary and nearshore waters, with no difference between wild and hatchery fish. The migration in marine water showed an early offshore movement and a strong northward and westward orientation, and all fish exited the Strait of Juan de Fuca rather than the Strait of Georgia. The findings support research suggesting that declines in wild and hatchery steelhead populations may be caused primarily by factors in the early marine period.

Keywords Behavior · Migration · *Oncorhynchus mykiss* · Survival · Telemetry

Introduction

Anadromy is a defining life history trait in salmonid fishes, allowing them to take advantage of foraging opportunities at sea, and facilitating gene flow among spawning populations (Quinn 2005). Juveniles of most salmon species rear in freshwater and migrate

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downstream through a series of ecotypes, from rivers to brackish and tidally influenced estuaries, to protected, nearshore marine areas, and finally open marine waters along the continental shelf or offshore regions. This period is a critical life stage for juvenile salmon as they experience major physiological changes (Clarke and Hirano 1995) but little is known about behavioral changes during movement through changing physical and biological environments, and whether particular behaviors can influence survival. High mortality rates have been observed during this early migration period that can strongly affect adult returns (Holtby et al. 1990; Ward 2000; Pearcy 1992). Survival rates of wild salmonid smolts are often higher than those of hatchery-produced fish (Raymond 1988; Chittenden et al. 2008; Melnychuk 2009a; Moore et al. 2010) but there are many possible explanations for this difference, including but not limited to behavior patterns. Behavior and movement rate differ between species, populations, rearing types, and fish of different body size in river, estuary and marine environments (Saloniemi et al. 2004; Melnychuk et al. 2010; Drenner et al. 2012; Chapman et al. 2012). Differences in migratory behavior could affect foraging success and survival through timing of movement (diel and tidal cycles), direction of movement (compass orientation and responses to tides), habitat (nearshore or offshore), migration route and timing within the season (Quinn 2005; Chittenden et al. 2008; Scheuerell et al. 2009; Melnychuk et al. 2010). Migration patterns may also explain differences in fitness between wild and hatchery fish, possibly due to differences in physiology, behavior, genetic background, and size (Holtby et al. 1990; Kostow 2004; Saloniemi et al. 2004; Chittenden et al. 2008; Melnychuk 2009a; Johnson et al. 2010).

Populations of steelhead (*Oncorhynchus mykiss)* in North America have declined in abundance in the past two decades (Ward 2000; Welch et al. 2000; Hard et al. 2007) but the causal factors are largely unknown. Puget Sound steelhead were listed as threatened under the U. S. *Endangered Species Act* (ESA) in 2007 (NOAA 2007) and steelhead abundance in this region is less than 4 % of historical levels (Gayeski et al. 2011). Until recently little was known about their seaward migration, as most monitoring methods were not well suited to study this life-stage. High mortality rates of steelhead were documented during the first month in the Strait of Georgia, British Columbia by Melnychuk et al. (2007) and Moore et al. (2010), and Welch et al. (2000) suggested that declines in wild and hatchery steelhead populations may be caused primarily by marine rather than freshwater factors. Studies from British Columbia have provided information on movement and survival of Pacific salmon exiting the Fraser River, and other, smaller rivers (Welch et al. 2004; Melnychuk et al. 2007) but there is a need for a comprehensive comparison of the behavior and survival of hatchery and wild fish released higher in the watershed during their entire migration in riverine, estuarine, and marine waters.

Our objective was to 1) quantitatively characterize steelhead behavior as they transition from riverine to estuarine to nearshore and open water habitats, and 2) compare the behavior of wild and hatchery origin fish in the river and, if different, determine at which point in the migration their behavior became similar. We predicted that wild smolts would survive at higher rates during their migration to the Pacific Ocean, begin their migration sooner after tagging as hatchery fish may need more acclimation time, travel faster than hatchery fish, and move more at night than hatchery fish, reducing predation risk. Upon entering the estuary wild fish were predicted to show a shorter period of delay, and migrate through Puget Sound more rapidly and by more direct routes than hatchery fish. We also predicted that both groups would alter their behavior to become progressively more day-active, as smolt migrations in rivers are typically nocturnal whereas adults tend to be more active in the daytime (Ruggerone et al. 1990).

Methods

Study area

Puget Sound is a large (3,700 km^2) interior marine system in western Washington, USA, bordered by British Columbia to the north (Fig. 1). Its physical attributes have been extensively described (Strickland 1983; Moore et al. 2008; Sutherland et al. 2011). Puget Sound is oriented north to south, and Admiralty Inlet is considered the northern extent and outlet of Puget Sound, connecting it to the Pacific Ocean through the Strait of Juan de Fuca, and to the Strait of Georgia. The average depth of Puget Sound is 62.5 m at mean low tide with average surface water temperatures of 12.8 °C in summer. The tidal range varies from 2.4 m at the north to 4.6 m in the south, producing strong currents in constricted areas between basins. Flow is dominated by tidal currents of up to 1 m/s in Strait of Juan de Fuca and 1–2 m/s at Admiralty Inlet, decreasing to approximately 0.5 m/s in central Puget Sound. There are a series of inlets, islands, and passages on the west side and large bays on the east side, including Elliott Bay at the mouth of the Green-Duwamish River.

The Green-Duwamish River flows from elevations over 1,500 m (Fig. 1) through the city of Seattle into Elliott Bay (Table 1). The Duwamish River is the 16 km estuarine portion and the Green River is the entirely freshwater portion (126 km). The Duwamish River has been extensively modified, with over 98 % of freshwater and intertidal habitats lost to development and maintenance of the river as a navigation channel. The estuary was defined as beginning at the upper extent of tidal influence (i.e., the Duwamish River) and ending at edge of the river delta. Areas external to the estuary were defined as marine waters, separated into shoreline (< 18 m deep) and offshore waters. The Duwamish estuary has three components. The lower estuary (RK 0–4) has two main waterways; the main channel and east channel (RK 1.2), and is most heavily influenced by

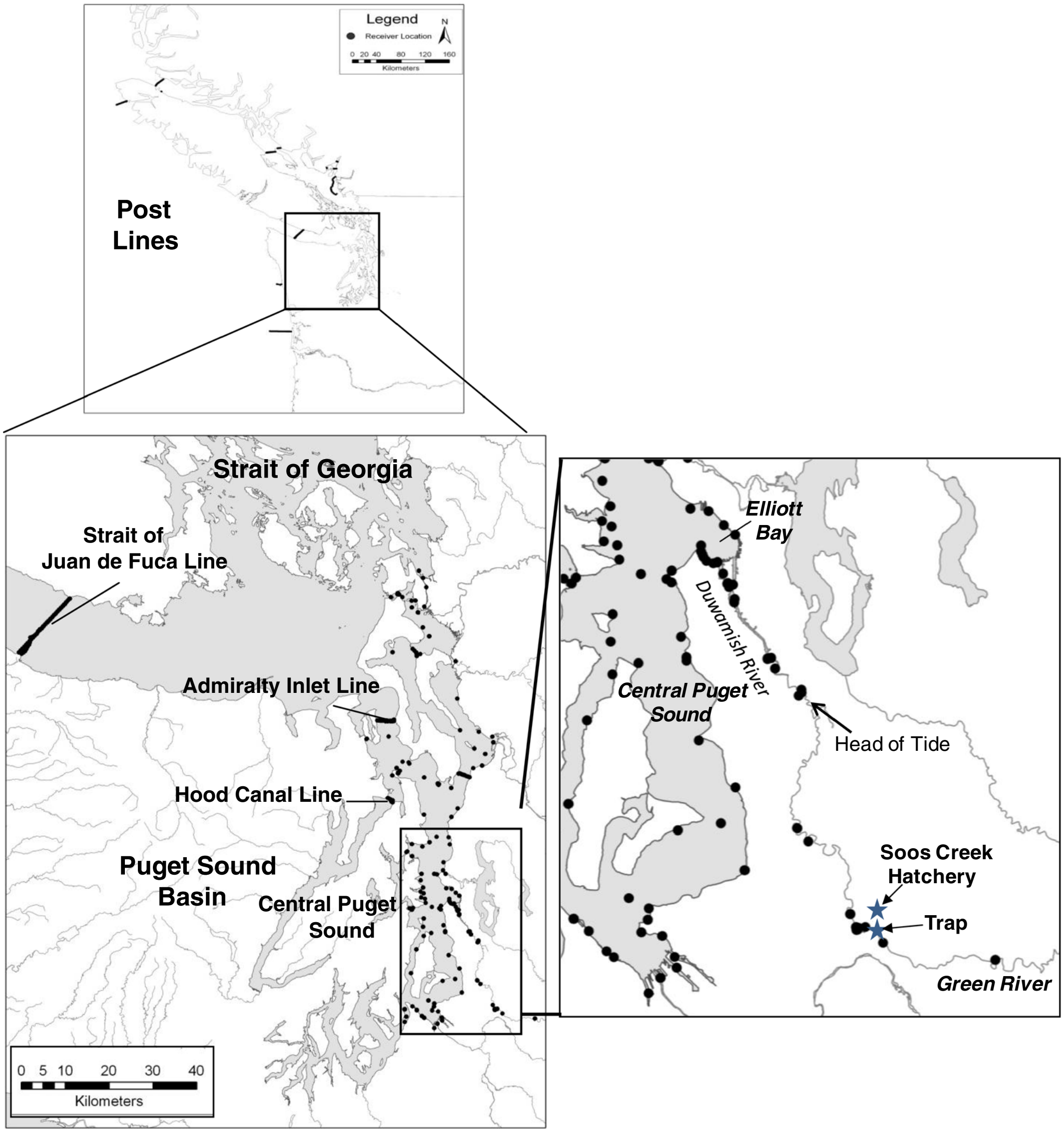


Fig. 1 Receiver lines in the Salish Sea and coastal waters near Puget Sound deployed and maintained by the POST Project (*top*) and receiver lines and single receivers in Puget Sound and Strait of Juan de Fuca (*bottom*). Receivers and tagging and release locations (*stars*) in the Green and Duwamish Rivers inset shown side inset

Table 1 Number of receivers by river and marine segment or major geographic area and year

Segment	2006	2007	2008	2009
Middle Green River (RK 48–55)	2	3	2	2
Lower Green River (RK 17–48)	1	1	2	2
Duwamish River Estuary (Upper RK 4–16, Lower RK 0–4)	6	11	11	9
Elliott Bay (single receivers)	3	6	12	10
South Central Puget Sound (Elliott Bay south to Tacoma)	9	8	12	18
North Central Puget Sound (Elliott Bay north to President Point)	16	17	32	15
Admiralty Line (06-07 Kitsap Peninsula to Whidbey I.) (08-09 Marrowstone to Whidbey I.)	5	3	15	15
Strait of Juan de Fuca Line	31	31	31	31

tides and saltwater. The middle estuary (RK 4–10) terminates at the end of the navigation channel, and the upper estuary (RK 10–16) has decreasing influence of tides and is primarily fresh water. The lower Green River (Tukwila to Auburn, RK 16–51) has few tributaries and little or no connection to the floodplain as a consequence of human development of the riparian area. The middle Green River (RK 51–72) has the most complete connection to the floodplain with accumulation of large woody debris, a meandering channel, and numerous side channels. At RK 53, Soos Creek meets the Green River, and approximately 1.5 km upstream is the Washington Department of Fish and Wildlife (WDFW) Soos Creek Hatchery.

Steelhead tagging and release

Wild and hatchery-origin steelhead smolts were tagged in 2006–2009. A floating screw trap (Seiler et al. 2002) was used to capture downstream migrating wild steelhead smolts at RK 55. Wild fish were trapped as they migrated at night, tagged the next morning, held in the live trap at the capture site and released in the evening in May and June, around the peak of migration in this river. Wild smolts are predominately 2 years of age, are progeny of wild and hatchery parents, and average 150 to 175 mm in length. At the Soos Creek Hatchery, adult steelhead (non-native Chambers Creek stock) are spawned between the January and March and the progeny are transferred to ponds in April where they are reared for 1 year. There they are maintained on ambient photoperiod, raised in spring water, fed commercial diets and then moved to surface waters prior to release at an average size of 201 mm and 75 g. Smolts were tagged 1 week before release, and then released from the hatchery during the day on April 30 or May 1, as is typical practice at this facility.

Steelhead smolts (n=187 wild and 150 hatchery) were tagged by surgical implant (e.g., Moore et al. 2010) using Vemco V7-2 L (1.6 g, 7 mm diameter, and 18.5 mm length) and V7-4 L (1.8 g, 7 mm diameter, 20.5 mm length) acoustic tags. The tagged fish were well within the normal size range but above average for the populations so that the tags were<3 % of body weight, corresponding to fish at least 165 mm and 60–85 g, depending on tag size (see also Moore et al. 2012). This was conservative, relative to the standards used by other investigators (e.g., Winter 1996; Welch et al. 2004). The hatchery fish tended to be larger than wild fish (hatchery mean length=191.3 mm (± 1.0 SE) and weight=66.2 g (± 1.0 SE) vs. wild mean length=184.4 (± 1.2) and 62.4 (± 2.3) and there was variation in size among years as well (ANOVA P<0.001).

Receiver deployment and retrieval

The objective of the receiver placement was to achieve a high probability of detecting smolts migrating from release through freshwater and from Puget Sound to the Pacific Ocean. In all years two or three receivers were deployed in the middle Green River near Auburn, one or two in the lower river, and six to 11 along the length of the Duwamish River from Tukwila to the mouth (Table 1). A combination of receivers (VR2, VR2W, and VR3) were deployed at shoreline and offshore sites in Elliot Bay and in all major bays and river deltas in Puget Sound (Fig. 1; Table 1). A line of receivers was deployed at Admiralty Inlet in 2006 (VR2), 2008 (VR2) and 2009 (VR3) at the outlet of Puget Sound, as was a line of receivers at Possession Sound, the outlet to Whidbey Basin, in 2006 (VR2) and 2008 (VR2), and at the outlet to Hood Canal from 2006 to 2009. The distance of receivers from the Duwamish River to Admiralty Inlet ranged from 48 km (2006–2007) to 62 km (2008–2009). The Pacific Ocean Tracking Project (POST; Welch et al. 2002) maintained receiver lines at the Strait of Juan de Fuca, the northern Strait of Georgia, northern Vancouver Island, and Queen Charlotte Strait (Fig. 1). The receiver spacing of these lines were based on potential detection range of a V9 (400-m) or V7 (200–250 m) tags. All Puget Sound lines in 2006 and POST lines outside of Puget Sound were designed for V9 tags (800-m spacing between receivers) while Puget Sound lines were designed for V7 tags (400-m) in all other years. Data from other researchers were collected either through direct contact or from online databases (hydra.sounddatamanagement.com/; www.postcoml.org/). In 2006, boat surveys were conducted three times over 2 months in the river from 10-km above the release site to 20 km below to identify potential mortalities or fish that did not migrate.

Analyses were designed to describe steelhead behavior and to estimate survival through five segments of the migration route corresponding to distinct habitats: 1) middle Green River, from the release site to Auburn (RK 55–48); 2) lower Green River (Auburn to Tukwila, RK 48–16); 3) Duwamish estuary (Tukwila to river mouth, RK 16- 0); 4) Puget Sound (Duwamish River mouth to Admiralty Inlet, ~ 60 km); and 5) Strait of Juan de Fuca, from Admiralty Inlet to the line of receivers across the Strait of Juan de Fuca, ~ 110–124 km from the river mouth. For some analyses the two segments in the Green River were combined and categorized as in-river, with the other segments referred to as estuary, Puget Sound, and Strait of Juan de Fuca.

Survival analysis

Cormack-Jolly-Seber (CJS) mark-recapture methods (Lebreton et al. 1992), adapted for spatial analysis (see Melnychuk and Walters 2010), were used to estimate apparent survival probabilities (ϕ), and detection probabilities (p) for steelhead smolts at five points: lower Green River (LR), Duwamish River estuary (EST), nearshore (NS), Admiralty Inlet (AI), and the Strait of Juan de Fuca (JDF; Fig. 1, Table 1). The CJS model uses maximum likelihood techniques to simultaneously estimate the probability of survival and detection at the end of each migration segment. Migration segments were defined based on the deployed receivers, and are referred to as point of release (PR) to LR (7 km), LR to EST (32 km), EST to NS (16 km), NS to AI (42–58 km, mean 50 km), and AI to JDF (110 km). Overall freshwater survival was estimated as the product of the PR-LR and LR-EST survival probabilities, and early marine survival was estimated as the product of the EST-NS, NS-AI, and AI-JDF survival probabilities. The standard errors for these products were calculated using the delta method (Cooch and White 2010). The R package RMark (Laake and Rexstad 2007) was used to construct ϕ and p models for the program MARK (White and Burnham 1999). Detection data from all 337 tagged individuals were incorporated into the MARK models.

Several candidate models were constructed using different variables to estimate steelhead smolt survival to and detection at each receiver line. Akaike's Information Criteria (AIC) were used to identify the set of variables that most parsimoniously explained the variation in survival and detection (Burnham and Anderson 1998). Goodness-of-fit to the CJS model, as measured by the variance inflation factor ĉ, was tested using the median ĉ method (Cooch and White 2010). The variance inflation factor was high ($\hat{c}=3.18$), but modeling results were adjusted accordingly to compute AIC values that compensate for extra-binomial variation and small sample sizes ($QAIC_c$). The detection probability portion of each model was parameterized to represent varying p at each receiver line. Year was tested as a source of variation in p at all receiver lines, and average yearly Green River flow during the tagging period (May 1–June 15, covariate), measured at RK 51.5 (USGS 12113000), was tested as a source of variation at the LR line (Table 2). Two covariates, length (L) and rearing type (rear) were included in some ϕ sub-models as linear or multiplicative terms in relation to the migration segment variable either with or without a "year" factor. A separate term was also included in each model to estimate a separate detection probability at Admiralty Inlet in 2008 and 2009, when 10–12 more receivers were deployed than in 2006 and 2007. All p models were first tested in combination with a general ϕ model (Table 2). The p model with the lowest QAICc was then used to test all ϕ models to determine the most likely model structure.

The CJS model uses subsequent detection occasions to estimate p for each previous occasion; therefore, ϕ and p are confounded for the last receiver line. To address this problem, empirically derived estimates from a similarly sited and configured receiver line were used to fix p at the JDF line (Melnychuk 2009b; Welch et al. 2011). Melnychuk (2009b) calculated mean and 95 % confidence limit estimates of p for V7 VEMCO tags passing a receiver line spanning the Strait of Georgia, British Columbia, in 2004, 2005, 2006, and 2007, so an average of the 2005–2007 values (2004 was an anomalous year) was used for all years to fix the value of p for the JDF line in our models ($p_{JDF,\ \mathrm{fixed}}=0.685$). All other estimates of ϕ and p and associated standard errors were derived from the model with the lowest $QAIC_c$ (Table 2).

Table 2 MARK Model results showing all models tested to determine which factors likely affected detection (top panel) and survival (bottom panel) probability

	Number of parameters	QAICc	ΔQAICc	Weight
Model (φ constant)				
φ(~segment)p(~segment×flow)	11	442.982	0	0.618
φ(~segment)p(~segment×flow+year)	14	444.049	1.07	0.362
φ(~segment)p(~segment×year)	22	450.357	7.375	0.015
φ(~segment)p(~segment+year)	13	452.787	9.805	0.005
φ(~segment)p(~segment×flow×year)	26	458.787	15.805	0.000
φ(~segment)p(~segment)	10	490.091	47.109	0.000
Model (*p* constant)				
φ(~segment+rear)p(~segment×flow)	12	441.613	0.000	0.375
φ(~segment+rear+length)p(~segment×flow)	13	442.730	1.117	0.215
φ(~segment)p(~segment×flow)	11	442.982	1.369	0.189
φ(~segment+length)p(~segment×flow)	12	444.784	3.171	0.077
φ(~segment+year+rear)p(~segment×flow)	15	445.542	3.929	0.053
φ(~segment+year)p(~segment×flow)	14	445.939	4.326	0.043
φ(~segment+year+rear+length)p(~segment×flow)	16	447.386	5.774	0.021
φ(~segment+year+length)p(~segment×flow)	15	447.995	6.382	0.015
φ(~segment×rear+length)p(~segment×flow)	17	449.728	8.116	0.006
φ(~segment×rear+year)p(~segment×flow)	19	452.640	11.027	0.002
φ(~segment+rear+year+length)p(~segment×flow)	20	454.513	12.900	0.001
φ(~segment * year+length)p(~segment×flow)	27	462.676	21.063	0.000

Factors tested in detection probability (p) models included migration segment (segment), annual average river flow (flow), and annual variation (year). Factor variables year and rearing history (i.e., hatchery or wild; rear), and a continuous fork length variable (length) were tested in survival (φ) models

Travel rate and migration timing

Travel rate (km/d) was calculated for each fish in each segment as the time from last detection at one site to the first detection at the next site over the segment's migration distance. The shortest distances were calculated between in-river arrays using river length and between marine lines or individual receivers in nearshore areas using the program AquaTracker (Reyes-Tomassini et al. 2011). Freshwater (LR-EST) and estuarine (EST-NS) travel rates (km/d) were calculated by subtracting the time of last detection at an upstream receiver line from the time of first detection at the downstream receiver line, then dividing that value by the distance between the two lines. Too few fish were detected on the NS, AI and JDF receiver arrays to analyze travel rates for the entire NS-AI or AI-JDF segments so detections from single receivers located throughout these two segments were utilized. Travel rate in the NS was calculated using the time between detections at two or more receivers at least 2-km apart divided by the distance between those two receivers. Factors affecting freshwater, estuarine, and marine travel rate were explored by constructing and comparing several general linear models. Candidate models used travel rate (km/d) as the response variable, and included all linear and multiplicative combinations of rearing type (i.e., hatchery or wild; "rear"), year ("year"), and length ("L"). Marine travel rate models included a factor variable ("area") to designate whether the rate was calculated in nearshore areas (6 to 40 km from the estuary), Admiralty Inlet, or the Strait of Juan de Fuca. Candidate models for each migration segment were compared using AIC_c (Burnham and Anderson 2002).

Several aspects of travel and residency were measured to evaluate migration behavior. Migration timing was examined by comparing the initial date of downstream migration after exit from the middle Green River for each individual detected at that receiver line. The migration period was bracketed for the middle Green and lower estuary using the minimum, 1^{st} quartile, median, 3^{rd} quartile, and maximum dates of detection. A one-way ANOVA was used to test whether mean travel rates to the estuary for wild fish by differed release week (i.e., first week of tagging was week 1). We defined the estuary residence period from the first detection at the upper estuary to the last detection in the estuary. A linear regression of mean river flow and the proportion of fish using the east channel assessed the tendency of fish to use this secondary exit from the estuary. The residence period in Puget Sound was defined from the last lower estuary detection to the last detection at Admiralty Inlet, and the ocean-entry migration window was the number of days from first to last detection at the JDF line.

Fish behavior on diel and tidal time scales

The diel and tidal patterns of movement were determined using the detections at fixed receivers. Following the method described by Chamberlin et al. (2011), the initial detection at a receiver after a period without detections and the last detection at that receiver if more than 1 h elapsed between these detections were discrete movement events. These "first" and "last" detections were clearly a small subset of all movements but, given the number of fixed receivers, they provided many movement events for analysis with respect to time of day and stage of tide. Movement events were binned by hour of the day for analysis. The detections were considered to have occurred in the day if they were between sunrise (dawn) and sunset (dusk), and night if they occurred after dusk and before dawn as determined by U.S. Naval Observatory data for Bangor, Washington. Tidal currents (hourly) for a nearby nearshore station (Nobeltec Tides and Currents Pro, v. 3.3) were used to evaluate movements relative to tidal cycles. Tides were categorized tides by current direction and speed for ebb (outgoing, predicted current velocity>0.25 m/s), flood (incoming, velocity>0.25 m/s), and slack (velocity<0.25 m/s). The first and last detections at estuary and nearshore receivers or arrays were used to evaluate the influence of diel period and tidal stage on movements.

The Watson Test (Watson 1962; Zar 1999) indicated that there were no significant difference between the timing of detections for hatchery and wild fish in freshwater or nearshore habitats ($U^2=0.11$, $P>0.2$); therefore, the data were pooled to assess changes in diel activity. Rayleigh's Uniformity Test (Zar 1999) was used to test the null hypothesis that fish movements were distributed uniformly over a 24-h period. The Watson-Williams F-test (Fisher 1993; Zar 1999) was used to compare paired hourly movement patterns between hatchery and wild fish (by migration segment) to determine if their timing differed significantly as they transitioned through these shorter migration areas both at reach (river, estuary, and nearshore) and sub-reach scales (middle Green, lower Green, upper estuary, lower estuary, and nearshore). The chi-square test for goodness-of-fit was used to test the hypothesis that fish movement was independent of the tidal phase and whether it varied by day or night periods.

Results

Receiver detection effectiveness

The probability of detecting transmitters using pooled receivers varied along migration segments from river to nearshore areas. The model with the lowest $QAIC_c$ for p included the segment variable and an additive "flow" term to constrain the LR detection probability with average yearly flow rates (p (segment+flow), Table 2). The difference in QAICc between models with and without yearly variation was small (ΔQAICc=1.07), so separate yearly detection rate estimates were not used. The lower river detection rate was estimated at 70.5±4.1 % but the detection rates at the estuary (94.8±1.8 %) and nearshore (98.0±2.0 %) lines were much higher. As expected, the Admiralty Inlet line had a lower estimated detection rate in 2006 and 2007 (33.9±11.4 %) than in 2008 and 2009 (54.3±20.5 %) when more receivers were present. The Strait of Juan de Fuca line detection rate was fixed at 68.5 %. A total of 184 smolts were detected at lower river receivers, 244 in the estuary, 154 at nearshore receivers, 41 at Admiralty Inlet, and 16 at the Strait of Juan de Fuca. Due to the lower probability and higher variability in detections in the river, estuary detections were used to estimate in-river survival rates for 2008 and 2009. Estuary detections were also used for analysis of travel time in freshwater and 2 years with high detection probability (2006, 2007) to assess travel times in the lower river.

Survival

The survival portion of the model with the lowest $QAIC_c$ included just the segment and rearing type variables (ϕ, segment+rear) (Table 2), indicating different survival rates for each migration segment and higher survival rates for wild fish (Table 3). The reduced model not including the rearing factor had a similar $QAIC_c$ (Δ $QAIC_c$=1.369), though the model estimating different survival rates for hatchery and wild smolts was twice as likely when considering the model weights (Table 2). Yearly variation in

ϕ was not evident ($\Delta QAIC_c=3.93$). Length was included in the model with the second lowest $QAIC_c$ ((ϕ (segment+rear+length), Δ $QAIC_c=1.117$, Table 2), and therefore may have an additive effect on survival probability of steelhead smolts. The coefficient for length in that model was positive (0.009), meaning that larger smolts experienced a slightly higher probability of survival than smaller smolts. Survival probabilities of both hatchery and wild smolts tended to be lower in the estuary and marine environment than in freshwater segments of the migration route (Table 3; Fig. 2). The distance based instantaneous mortality rates (% mortality per km) were highest from release to the lower river (average 2.0 % wild, 3.3 % hatchery) and from the estuary to the nearshore (2.5 % wild; 3.8 % hatchery). The instantaneous mortality over time (mortality/d) was highest in the estuary (wild 2.5 %, hatchery 3.8 %), lowest in freshwater (wild 0.6 %, hatchery 1.0 %), and intermediate in nearshore (wild 0.9 %, hatchery 1.3 %). The composite freshwater survival probability estimate from release to the estuary was more than 13 times higher than the marine survival estimate (estuary to Strait of Juan de Fuca) for hatchery smolts, and nearly seven times higher the one for wild smolts (Table 3). The cumulative survival rate from release to the Strait of Juan de Fuca was 9.7 % for wild and 3.6 % for hatchery smolts (Table 3).

Travel rate and time

Wild fish travelled faster than hatchery fish through all migration segments except marine waters, where they were similar (Fig. 2), and this was the most important factor describing freshwater travel rate. Hatchery smolts travelled much more slowly downriver than wild fish (mean=4.4 km/d±SE 0.4 vs. 15.1 km/d±SE 1.1). The model including rearing type and length (FW rate~ rear+length) was also supported by the data ($\Delta AIC_c=1.67$), so length may have had a small effect on freshwater travel rate, with larger fish migrating faster. Travel rates from release to the estuary varied by tagging week for wild fish, with faster travel rates later in the tagging period. There was a significant decrease in the average travel time from week 1 (7.2 km/d, travel time 6.3 days±SE 0.6) to week 4 (19.1 km/d, 2.8 days±SE 0.4; ANOVA; $P<0.01$).

Smolts moved more rapidly through some of the river segments than others. In 2006 and 2007 hatchery and wild fish were tracked over shorter migration segments from point of release to middle Green River, through the lower Green River to the estuary, and through the estuary. Fish from both groups resided for the longest period and traveled slowest in the reach immediately below the release site, with hatchery fish traveling slower (mean=2.4 km/d, SE±0.4) than wild fish (mean=3.7 km/d, SE±0.8). Then, wild fish migrated rapidly between the middle and lower sections (mean=41.4 km/d, SE±3.3); hatchery fish migrated more slowly (mean=20.2 km/d, SE±2.4) between the sections. Average travel rates in the estuary for 2006–2007 were similar for hatchery and wild fish ($mean_{hatchery}=10.8$ km/d, SE±1.5, $mean_{wild}=13.8$, SE±1.8).

Estuarine travel rate was best explained by an interaction between rearing type and year (Estuary rate~ rear×year). Hatchery and wild smolts traveled at similar rates through the estuary in 2006 ($mean_{hatchery}=9.4$ km/d±SE 2.9; $mean_{wild}=10.3$ km/d±SE 2.2) but hatchery smolts travelled more slowly than did wild smolts in 2007 ($mean_{hatchery}=11.5$ km/d±SE 1.8; $mean_{wild}=17.5$ km/d±SE 2.6) and in 2008 ($mean_{hatchery}=10.3$ km/d±SE 2.7; $mean_{wild}=22.4$ km/d±SE 2.2). No hatchery smolts were tagged in 2009 but wild smolts traveled at a similar rate to 2006 and 2008 ($mean_{wild}=10.4$ km/d±SE 1.3). Length did not influence estuarine

Table 3 Survival probability (percent) estimates of steelhead trout smolts±SE based on the model with the lowest $QAIC_c$ value (ϕ (segment+rear), p (segment+flow)

Migration segment	Hatchery smolts	Wild smolts
PR (Point-of-Release)-Lower River (LR)	79.6±3.0 (−3.3)	86.9±2.2 (−2.0)
LR-Estuary (EST)	86.4±3.2 (−0.5)	91.5±2.1 (−0.3)
EST-Nearshore (NS)	54.3±4.2 (−3.8)	66.9±3.5 (−2.5)
NS-Admiralty Inlet (AI)	51.7±19.5 (−1.3)	64.6±18.2 (−0.9)
AI-Juan de Fuca (JDF)	18.6±8.1 (−1.5)	28.1±10.2 (−1.2)
Freshwater (PR-LR×LR-EST)	68.7±3.5 (−1.0)	79.5±2.1 (−0.6)
Early Marine (EST-NS×NS-AI×AI-JDF)	5.2±1.7 (−1.8)	12.1±4.4 (−1.3)

Instantaneous mortality rates (mortality/km) are shown in parentheses

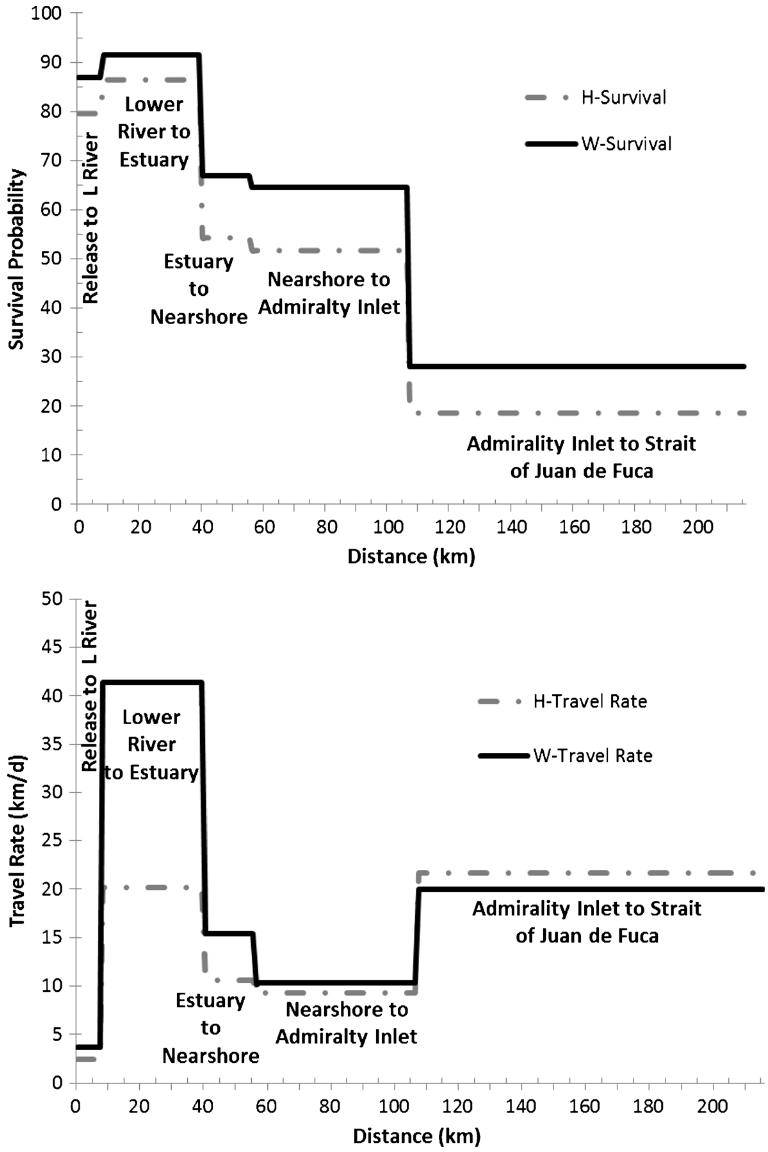


Fig. 2 Survival probability (mean, *top panel*) and travel rate (mean, *bottom panel*) by distance for wild (*W*) and hatchery (*H*) smolts from release to Strait of Juan de Fuca. Travel rates for freshwater segments use 2006–2007 data to differentiate release to the lower river and lower river to estuary

travel rate (Δ AIC_c=2.863). Wild smolts tended to spend less time in the estuary than hatchery smolts but the difference was not significant ($P>0.15$, $\text{mean}_{\text{wild}}$= 1.1 days±SE 0.2; $\text{mean}_{\text{hatchery}}$=1.9 days±SE 0.3). Some smolts moved back upstream on flood tides in the upper estuary, and hatchery fish did so more often (average 16 %) than wild fish (7.8 %); these fish had longer residence (average 4.7 days) compared to smolts that did not migrate upstream (1.2 days).

The best model for marine travel rate included only the area through which the fish were travelling. Mean travel rates in nearshore areas (9.5 km/d) and Admiralty Inlet (10.6 km/d) were similar, and much slower than the mean rate calculated for the Strait of Juan de Fuca (20.6 km/d). Fish length was included along with area in the next best model (Marine rate~area+length, ΔAIC_c=1.672), so may have had a small effect on travel rate within each marine area with larger fish migrating faster, though the model including just "length" performed poorly (Marine rate~length,ΔAIC_c= 12.011). Wild fish spent only 5.1 days (SE±0.7) and hatchery fish 7.5 days (SE±0.9) in Puget Sound, from the time they left the estuary.

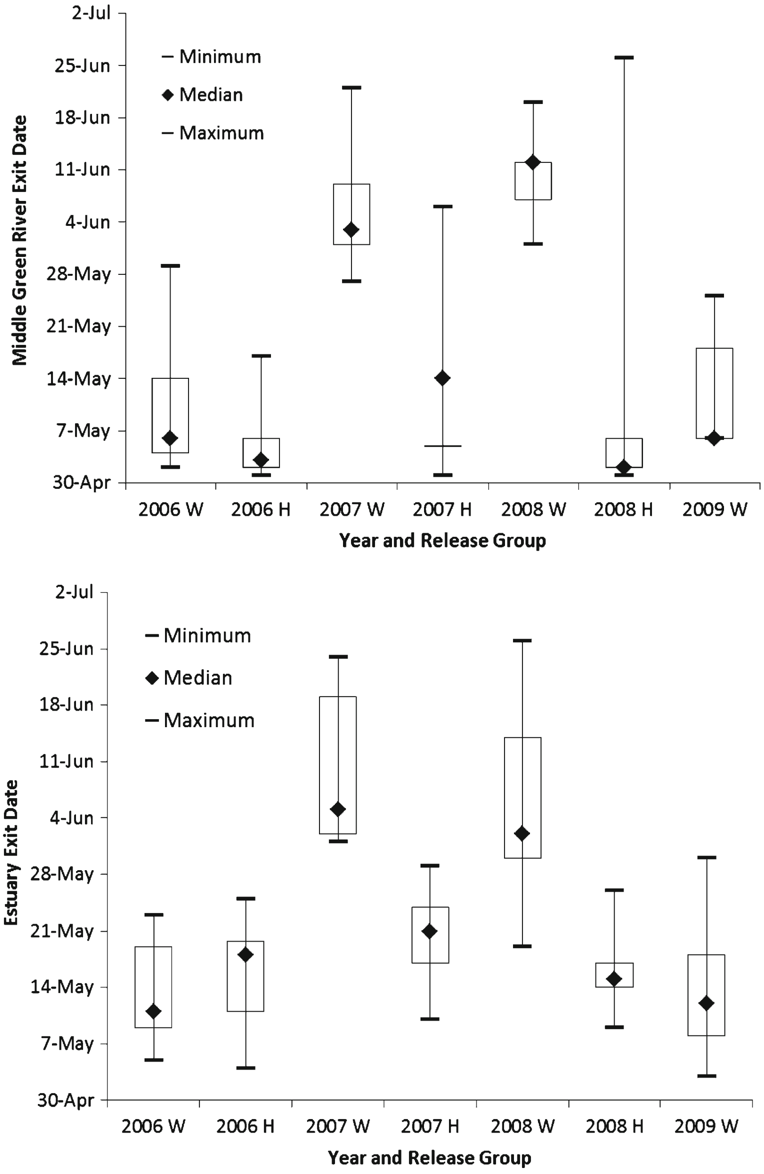
After entering marine waters, 99 % of the smolts migrated north through Puget Sound (only

1 % initially moved south) and then all fish moved west through the Strait of Juan de Fuca rather than continuing north through the Strait of Georgia. The timing of movement varied by release group and year as they migrated down the river and through the estuary but in general the hatchery fish migrated earlier than the wild fish, as a function of the dates of tagging and release (Fig. 3). The pooled timing for all tags at the JDF shows a migration window from first to last detection of 22 days in 2006, 36 days 2007, 49 days 2008, and 23 days 2009.

Migration routes

At the exit from the Green River to the Duwamish River, the number of fish using the east channel or main channel varied by year but was similar in wild and hatchery fish. Pooled averages ranged from 6 % in 2007 to 31 % in 2009 and 53 % in 2008, and higher flows were associated with more fish using this secondary channel ($F_{1,2}=275$, $P<0.01$). Use of these channels affects the subsequent route in Puget Sound either along the shoreline or as movement offshore. In the years with highest flow (2008), fish using the east channel tended

Fig. 3 Migration timing (number of tags detected per day) of wild (*W*) and hatchery smolts (*H*) by year exiting the middle river (*top*) and the lower estuary (*bottom*). Box includes 1st and 3rd quartile



to use shoreline areas in Elliott Bay: 67 % of the fish detected in the east bay and 88 % in the west bay were first detected in east channel. In total 93 % of the wild fish detected along Elliott Bay shoreline areas in 2008 were detected in the east channel. In contrast, in 2009 only 33 % of wild fish detected in Elliott Bay were first detected in the east channel.

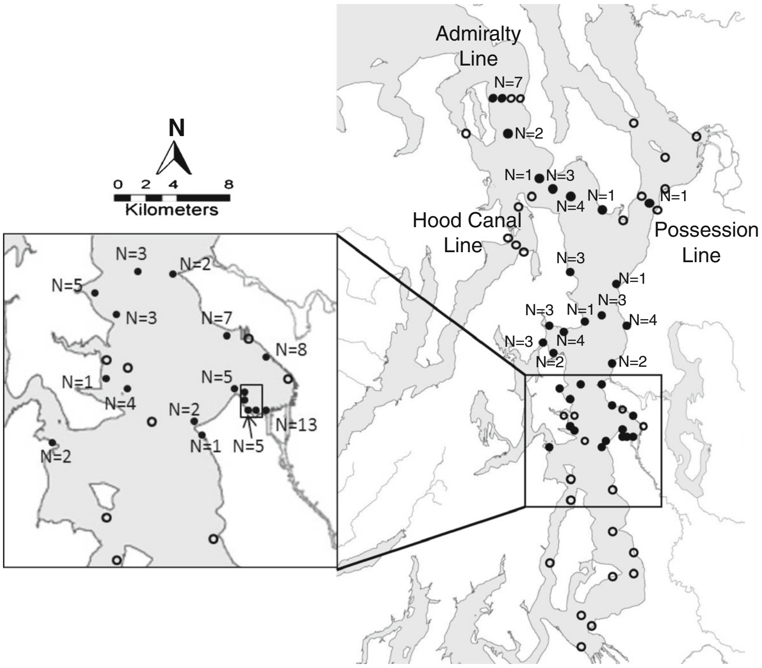
Irregularities in the shoreline may influence smolt migration paths. For example, at a major point (Duwamish Head) 2.5 km west of the river in 2006, 17 fish were detected only on the river side of the point but none were detected only on the marine side of the point (0.5 km west). Thus most fish were already moving off-shore and northward rather than following the shoreline west-ward around the point. Similarly, in 2008 13 fish were detected on the river side of the point but only two fish were detected west of the point.

In central Puget Sound the fish moved northward and westward (e.g., Fig. 4 illustrates the distribution of detections by receiver location for 2008). A few fish were detected south of Elliott Bay (1.5 % of wild and 0.6 % of hatchery fish were detected 7 km, and 1 % of wild fish up to 28 km south). Migration in central Puget Sound in 2008 and 2009 was predominately along the west shore (ca. 2/3 vs. 1/3 of detections on the east shore). The initial shoreline orientation in Elliott Bay (i.e., east or west shore) had no effect on whether the fish were eventually detected at Admiralty Inlet, so northward migration was accomplished without any bias from initial shoreline choice.

All fish detected exiting Puget Sound migrated through the Admiralty Inlet (i.e., none was detected using another route) and all fish detected migrated west through the Strait of Juan de Fuca rather than north through the Strait of Georgia. At Admiralty Inlet most smolts were off-shore or in the center of the channel; 81 % of detections in 2008 and 88 % in 2009 were at receivers at least 1.6 km offshore (i.e., the middle 50 % of the channel). At the Strait of Juan de Fuca, 31 receivers were deployed at the same locations each year across 21 km from Vancouver Island to the Olympic Peninsula. The distribution of smolt detections was equally divided between the shorelines and center of channel.

The most complete individual migration paths in Puget Sound were for two wild fish from 2008 and one hatchery fish from 2006. The wild fish both moved west and north and one was detected at Admiralty Inlet (120 km at 10.3 km/d, detected on 10 receivers) whereas the other used a more tortuous path (72 km, 6.2 km/d, detected on 7 receivers). These fish showed much slower net travel rates than other wild fish that exited Puget Sound and reached the Strait of Juan de Fuca line in 2008 at 20.1–34.2 km/d. The hatchery fish moved

Fig. 4 Number of individual tags detected by receiver location (*black circle* with number of tags detected, e.g. N=x; open circle receiver with no detections) in Puget Sound in 2008, lines of receivers do not show all receivers (legend and scale are for inset)



much slower (66 km, 2.3 km/d, detected on 10 receivers) than the wild fish but ultimately reached Admiralty Inlet. Each of these three fish was detected crossing the basin three times. Even with these multi-receiver tracks there were gaps from days to a week with no detections, implying even more complex movements or holding in some areas. Most fish tracked in Puget Sound areas were detected on only 1–4 receivers, providing less complete histories.

Diel behavior

There were approximately 15.5 h of light and 8.5 h of dark (65 % day, 35 % night) during the spring months when the fish were migrating. Overall activity patterns inferred from the discrete movement events varied by migration segment ($P<0.001$), beginning as primarily nocturnal in the riverine segments (70 % night), progressing to nearly equal day (48 %) and night (52 %) in the upper estuary. Once smolts reached the lower estuary and Puget Sound their movements approximated those expected for daylight in May and June (68 % day, 32 % night). There were significant differences in diel timing between the lower Green River (90 % night movement) and upper estuary (52 % day, 48 % night, $P<0.001$) and the upper to lower estuary (68 % day, 32 % night) ($P<0.05$) but no difference from the middle to lower Green ($P=0.355$) and from the lower estuary to Puget Sound ($P=0.24$). There were peaks in activity within the diel period, shifting from near midnight in the middle Green River, to near 01:00–02:00 h in the lower Green River, near dawn in the upper estuary, late morning in the lower estuary, and throughout the day in Puget Sound (Fig. 5). Movements were non-uniformly distributed in all freshwater, estuary and Puget Sound migration segments for all fish except hatchery fish in the lower estuary (Raleigh's $_{Z=0.05}$, $P<0.05$). There were differences in the primary period of movement (mean angle) using paired and multiple hourly samples for release group by migration segment at the upper estuary and Puget Sound (Raleigh's $_{Z=0.05}$, P <0.001, Watson-Williams F Test, Fisher 1993; Zar 1999).

Wild and hatchery smolts moved in the estuary more frequently on the ebb tide and less frequently on the flood tide than expected as a function of the time of day in those tidal stages ($P=0.01$ wild, $P<0.0001$ hatchery) whereas in Puget Sound both groups moved in proportion to tidal periods ($P>0.4$). In migrating from the upper to lower estuary, the movements of wild fish transitioned from more frequent than expected movements at ebb tide in the upper estuary ($P<0.01$) to proportional in the lower estuary ($P=0.8$) whereas hatchery fish moved more often than expected on ebb tides in both estuary segments ($P<0.01$). In relation to diel and tidal period, wild smolts tended to move through the estuary and Puget Sound in proportion to the expected periods of current direction during the day ($P>0.1$ estuary and Puget Sound) and night ($P=0.2$ Puget Sound), except in the estuary at night ($P<0.05$) where they moved more during ebb tides (Table 4). Hatchery fish in the estuary moved more often on ebb tides and less on floods than expected during both the day ($P<0.0001$) and night ($P<0.05$) but in the Puget Sound did not differ in the frequency of expected tides ($P=0.44$ day, $P=0.9$ night).

Discussion

Survival

Wild Green River steelhead smolts survived at higher rates than hatchery smolts through all migration segments (Fig. 2) but rates were generally low during the 215 km migration from release to the Strait of Juan de Fuca (wild smolts=9.7 % survival, 1.1 %/km mortality rate; hatchery smolts=3.6 % survival, 1.5 %/km mortality rate) compared to other studies of steelhead in the region. Moore et al. (2010, 2012) and Melnychuk et al. (2007) used similar mark-recapture models to estimate steelhead survival rates from release to Salish Sea exit and found survival rates ranging from 28 % (wild) to 10 % (hatchery) for Hood Canal smolts from river release to Strait of Juan de Fuca (163–210 km) and 27 % for Cheakamus River, British Columbia wild smolts through the Strait of Georgia (155–230 km). In Hood Canal, the distance-based instantaneous mortality rate during the 13 km freshwater migration for the Skokomish River wild smolts was low (0.3 %/km) but was much higher for hatchery smolts (4.8 %/km). Mortality rates within Hood Canal (3.25–3.5 %/km) and between the Admiralty Inlet and Strait of Juan de Fuca lines (1–1.2 %/km) were similar for both groups (Moore et al. 2012). The high mortality rates for steelhead smolts migrating through the Salish Sea could limit overall productivity because they are on the order of the total marine mortality estimated from steelhead populations in general from earlier periods (Quinn 2005).

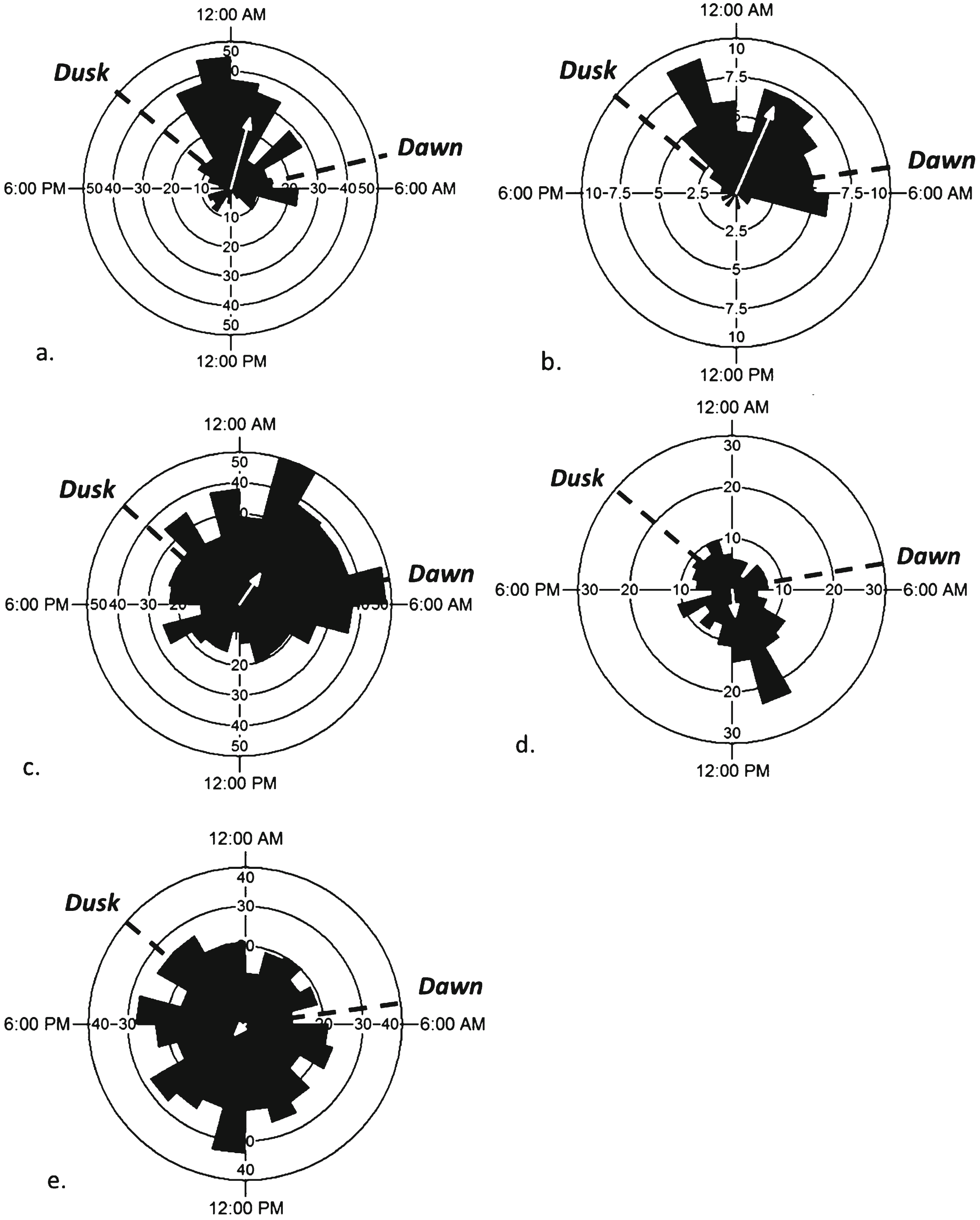


Fig. 5 Rose diagrams of hourly detections of all fish through migration segments **a** middle river (337 detections); **b** lower river (69); **c** upper estuary (638); **d** lower estuary (207); and **e** nearshore (470). The axis scale varies by segment and the *white arrow* shows mean vector

Table 4 Proportion of observed movements by hatchery and wild fish by day (top) and night (bottom) and tidal current period compared to the expected proportion with significance value

	Hatchery observed	Hatchery expected	P-value	Wild observed	Wild expected	P-value
Day						
Estuary						
Ebb	0.66	0.50	<0.0001	0.55	0.49	0.12
Flood	0.20	0.34		0.32	0.34	
Slack	0.14	0.16		0.14	0.17	
Nearshore						
Ebb	0.44	0.50	0.44	0.53	0.49	0.12
Flood	0.36	0.34		0.35	0.34	
Slack	0.20	0.16		0.12	0.17	
Night						
Estuary						
Ebb	0.58	0.47	0.04	0.56	0.48	0.02
Flood	0.26	0.34		0.24	0.32	
Slack	0.16	0.18		0.20	0.20	
Nearshore						
Ebb	0.46	0.47	0.9	0.52	0.48	0.2
Flood	0.33	0.34		0.24	0.32	
Slack	0.21	0.18		0.25	0.20	

These rates varied little between years, unlike the higher variability found in Oregon coastal rivers and estuaries (Romer et al. 2012), but without a longer period of record and larger samples it is difficult to interpret this difference. In comparison to the Puget Sound results, steelhead from the Napa River, California had lower mortality rates during the entire migration from release, through San Francisco Bay, to the ocean (0.67 %/km: Sandstrom et al. 2013).

In the present study, hatchery smolts survived at a consistently lower rate through all migration segments relative to wild smolts; there was a slight increase in survival relative to fish size and larger hatchery smolts migrated to the estuary at a faster rate. Higher probability of survival was reported for larger compared to smaller smolts in British Columbia's Keogh River steelhead (Ward et al. 1989) and other Pacific salmon species (Holtby et al. 1990; Henderson and Cass 1991), and for smaller smolts that reached a large size by feeding in a California coastal estuary (Bond et al. 2008).

While early marine survival may be important, and high mortality has been documented for Puget Sound smolts, further mortality takes place during the two or three subsequent years at sea prior to return as adults. The general perspective is that the additional mortality in the ocean likely declines as fish size increases over time (Ricker 1976; Quinn 2005). In contrast, smolt survival estimates from the POST array (16 %) in the first month out of the Salish Sea compared to the entire mortality from juvenile to adult returns (1–4 %) suggests that the cumulative mortality is 4–17 times greater in the ocean than in the Salish Sea (Welch et al. 2011). Survival rates for hatchery steelhead released in the Puget Sound region (e.g., Green River) were the lowest of any region in Washington State (Scott and Gill 2008), declining from 7.0 % for smolts entering the ocean in 1983 to 0.2 % in 1996, and remaining near that level since (Scott and Gill 2008). The low survival of Green River steelhead appears to be a combination of lower estuarine and early marine survival relative to other Salish Sea populations (Welch et al. 2004, 2011; Moore et al. 2012) and continuing low survival during ocean rearing for all populations.

Travel rates

The marine travel rates observed for Green River steelhead were consistent with previously published values. Welch et al. (2011) found that juvenile sockeye salmon (*O. nerka*) and steelhead migrated in the Salish Sea at rates corresponding to ca. 0.95 and 0.86 body lengths per second (BL/sec, respectively), consistent with the optimal migration speeds of 0.8–2.0 BL/sec calculated for small sockeye salmon (Brett 1995). Swimming speed estimates for Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*) smolts also averaged about 1 BL/sec (Finstad et al. 2005). Similar marine travel speeds were also observed for steelhead in a number of Washington and BC populations (Melnychuk et al. 2007; Moore et al 2010; Payne et al. 2010). The Green River smolt migration speeds varied by migration segment with wild fish migrating faster than hatchery fish in the river (0.93 vs. 0.27 BL/sec), more similar in the estuary (0.95 vs. 0.64 BL/sec), even more similar in Puget Sound (0.64 vs. 0.56 BL/sec) and accelerating as they exited the Strait of Juan de Fuca (0.99 (wild) and 1.11 (hatchery) BL/sec).

The mean travel rates of wild smolts were faster than those of hatchery fish from release to the estuary and from the upper to lower estuary. These differences may be related to the hatchery's release strategy, as all smolts were released at a single time each year (early May), irrespective of environmental conditions or any assessment of the physiological state of the fish. The release of hatchery fish into the river provided no period for learning and acclimation, and perhaps they were not physiologically ready to migrate (Gale et al. 2009; Lorenzen et al. 2012). Hatchery fish had the most variable and slowest travel rates near the release site; some fish immediately migrated downstream to the estuary but others remained near the release site for several days before leaving. Hatchery fish also had the slowest and most variable travel rate in the upper estuary, similar to behavior shown elsewhere (Kennedy et al. 2007). The hatchery smolts were released earlier than the wild fish, and wild migrants tagged earlier moved slower than later migrants but without controlled experiments involving both groups it is not possible to distinguish rearing effects from those related to time of year.

Estuaries are important rearing areas for a variety of juvenile salmonids during initial entry into marine waters (Thorpe 1994) but the importance of residency in nearshore waters is largely unknown for steelhead. The use of estuaries by steelhead is considered to be short relative to other smaller-bodied salmonids (Quinn 2005). The shorter estuary residence time of smolts considered physiologically prepared for ocean entry has been considered proportional to the probability of survival to the ocean (Schreck et al. 2006; Kennedy et al. 2007). In our study estuary residence time (wild 1.1 days SE 0.3, hatchery 1.9 days SE 0.4) was significantly less than river residence (wild 5.9 days, hatchery 16.4), thus consistent with the idea that steelhead do not remain long in estuaries. Telemetry studies in Hood Canal tributaries (Moore et al. 2010, 2012), and the Alsea and Nehalem rivers in Oregon (Clements et al. 2012; Johnson et al. 2010) also indicated short (1–2 days) estuary rearing period for wild and hatchery steelhead. Although migrants in Hood Canal spent little time in the estuaries, the average residence time for smolts in nearshore areas before exit from the canal was 14.7–17.2 days (travel rates 8.0–10.1 km/d) with 1/3 of these smolts backtracking substantial distances, suggesting that conditions within Hood Canal promoted retention of steelhead smolts (Moore et al. 2010). Green River smolts in this study resided in Puget Sound for a mean of 5.1 days (wild travel rate 15.3 km/d) or 7.5 days (hatchery travel rate 5.3 km/d). Unlike Hood Canal in this study there were few fish found south of the initial entry point into Puget Sound (1 %) with the large majority of fish moving westward and northward.

Migration route and direction

Our study provides new data on marine migratory behavior of steelhead during their migration from river to ocean. In British Columbia there may be species-specific migration routes through the Strait of Georgia, with some typically exiting northwards through Queen Charlotte Strait (Groot et al. 1989; Tucker et al. 2009), and others migrating westward through the Strait of Juan de Fuca (Trudel et al. 2009). Upon entry to Puget Sound a portion of wild and hatchery steelhead used local shoreline areas in Elliott Bay before moving offshore, after which almost all migrated west and north through Puget Sound and west to the ocean. The direction of travel after arrival in coastal waters may be important as shorter routes may reduce time and hence exposure to predators in coastal waters. Recent studies suggest that most steelhead from northern Vancouver Island and the lower mainland migrate north via Queen Charlotte Strait whereas southern populations may use both the northern and southern (Strait of Juan de Fuca) routes (Melnychuk et al. 2010; Welch et al. 2011). The current study and other telemetry research during the same years indicated that Puget Sound and Hood Canal steelhead migrated exclusively through the Strait of Juan de Fuca (Moore et al. 2010, 2012).

Timing and diel behavior

Drenner et al. (2012) noted there have been few studies of the diel behavior of smolts along their entire migration path through ecotypes from river and marine waters. Smolt migrations down rivers typically occur predominately at night, and particularly during periods with low water temperatures, with a transition to day-time activity as fish reach estuary waters (Godin 1982; Moser et al. 1991; Crittenden 1994; Ibbotson et al. 2006). Steelhead smolts generally follow this pattern in coastal rivers, moving primarily after dusk (Melnychuk et al. 2007; Johnson et al. 2010) but becoming diurnal once they reach the estuary (Ledgerwood et al. 1991), and these patterns were evident in the present study. In contrast, the movements of steelhead smolts in the Sacramento River did not show a strong diel pattern and they often moved during the day along the entire migration path (Chapman et al. 2012). In our study the movement period from river to the estuary was transitional from nocturnal to daytime, with approximately half the movements during day and night in the upper estuary, while movement through the lower estuary and marine water was mostly during the day, but in proportion to the amount of day. The transition at the upper estuary towards diurnal movement may be a response to the first exposure to tidal currents which alternate between up and downstream movements twice during the day vs. the downstream flows of rivers, and wild fish may make this transition more rapidly than hatchery fish. Johnson et al. (2010) found that hatchery steelhead tended to move downstream during daytime ebb and upstream during night-time flood tides whereas wild fish moved downstream regardless of diel or tidal period. Martin et al. (2009) suggested that as Atlantic salmon experience higher salinity moving through the leading edge of saltwater this induces a transition from passive, fluvial migration to a more active and seaward migration. In marine waters, adult steelhead are day-active and remain near-surface (Ruggerone et al. 1990; Nielsen et al. 2011).

Most of these previous studies relied on 1 to 2 years of study and reported on two segments of the migration path but our work spanned three (hatchery) and four (wild) years, and included movements along the entire course of movement from in-river release to the ocean. This study advances the understanding of how the migratory behaviour of wild and hatchery smolts may explain differences in survival during their river and early marine migration through Puget Sound. This understanding will be valuable in informing where data gaps exist to guide further examination of factors influencing early marine survival and longer-term smolt to adult survival. Although hatchery fish survived at lower rates through all migration segments, both rearing types experienced high initial mortality in the river, and in transitions from river to estuary and marine environments. Some of the reasons for the high mortality may be specific to the Green River and local marine areas (i.e., habitat modification, pollution and predators); however, the breadth of salmon populations experiencing low marine survival indicates a more general problem affects other steelhead populations and other salmonid species. It will be important to incorporate this loss into models of ocean survival to ensure that recovery planning options target the areas and factors most likely to yield benefits.

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