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Survival and behavior of juvenile steelhead trout (*Oncorhynchus mykiss*) in two estuaries in Oregon, USA

Jeremy D. Romer · Camille A. Leblanc ·
Shaun Clements · Jayde A. Ferguson ·
Michael L. Kent · David Noakes · Carl B. Schreck

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Abstract Anadromous salmonids are viewed as a prized commodity and cultural symbol throughout the Pacific coast of North America. Unfortunately, several native salmonid populations are threatened or at risk of extinction. Despite this, little is known about the behavior and survival of these fish as the juveniles transition from freshwater to the ocean. Our primary objectives were to estimate survival of juvenile steelhead migrating between trapping sites and the ocean and evaluate whether survival in the estuary varies temporally (within a year) or spatially (within and between estuaries) within the same distinct population segment. We also evaluated whether flow or fork length were correlated with survival and collected information on variables that have been demonstrated to affect smolt survival in other studies to lend insight regarding differences in survival estimates between basins. We compared run timing, migration rate, survival, condition factor, age composition and time of residence in the estuary for steelhead outmigrants from each basin and measured parasite loads in outmigrating steelhead to evaluate potential differences in parasite density and parasite community between basins. In 2009, we implanted acoustic transmitters in 139 wild steelhead smolts in two small rivers on the Oregon Coast. In general, only 40–50 % of the wild steelhead smolts tagged at upstream smolt traps were detected entering the ocean. The majority of mortality occurred in the lower estuary near the ocean. Wild steelhead smolts typically spent less than 1 day in

J. D. Romer (✉) · C. A. Leblanc · D. Noakes ·
C. B. Schreck
Department of Fisheries and Wildlife, Oregon State University,
Nash Hall Room 104,
Corvallis, OR 97331, USA
e-mail: Jeremy.Romer2@oregonstate.edu

J. D. Romer · S. Clements
Oregon Department of Fish and Wildlife,
28655 Highway 34,
Corvallis, OR 97333, USA

J. A. Ferguson · M. L. Kent
Department of Microbiology, Oregon State University,
Nash Hall Room 201,
Corvallis, OR 97331, USA

D. Noakes
Oregon Hatchery Research Center,
2418 East Fall Creek Road,
Alsea, OR 97324, USA

C. B. Schreck
Oregon Cooperative Fish and Wildlife Research Unit, U.S. Geological Survey,
Nash Hall Room 104,
Corvallis, OR 97331, USA

Present Address:
J. A. Ferguson
Alaska Department of Fish and Game, Division of Commercial Fisheries, Fish Pathology Laboratory,
333 Raspberry Road,
Anchorage, AK 99518, USA

the estuary in both basins. Using similar data from previous studies in the Nehalem and Alsea basins, we showed that survival appears to be negatively correlated with flow in most releases, and in 2009 fork length was not correlated with survival. Our observations provide baseline information on factors that could influence smolt survival through the estuary as well as smolt to adult survival in these basins, and emphasize the importance of monitoring smolt survival in the estuary.

Keywords Survival · Smolt · Estuary · Acoustic · Telemetry · Flow

Introduction

Several native anadromous salmonid populations throughout the west coast of North America are threatened or at risk of extinction (Nehlsen et al. 1991; Slaney et al. 1996). In Oregon, four populations of steelhead (*Oncorhynchus mykiss*) are currently listed as threatened by NOAA Fisheries (http://www.nwr.noaa.gov/ESA-Salmon-Listings). Efforts to recover these populations have focused primarily on the freshwater rearing phase and management of terminal harvest. Little is known about the survival and behavior of juvenile steelhead immediately prior to ocean entry. However, researchers have observed considerable spatial and temporal variation in behavior, physical condition, and survival during the outmigration (Stefansson et al. 2008; Johnson et al. 2010; Clements et al. 2011). The variation in behavior and condition is likely a key factor explaining differences in survival as juvenile salmon emigrate to the ocean (Schreck and Li 1991; Mesa 1994; Olla et al. 1995). Factors such as flow and/or turbidity (Gregory and Levings 1998; Emmett 2006), parasites (Jacobson et al. 2008; Ferguson et al. 2011), and disease (Barber et al. 2000; Schreck et al. 2006) affect both the behavior and survival of smolts. Thus, it is important to understand how variation in behavior and physical condition are driven by environmental variables and what effect these changes have on the survival of individuals and the population.

The Oregon coastal steelhead distinct population segment (DPS) includes the populations in the Nehalem and Alsea basins. Native steelhead in both basins are listed as ‘vulnerable species’ by the Oregon Department of Fish and Wildlife and ‘species of concern’ by NOAA Fisheries and regulations are currently in place to protect native winter run steelhead from harvest. Previous studies in the Nehalem (Schreck et al. 2002; Clements and Schreck 2003; Clements et al. 2011) and Alsea basins (Johnson et al. 2010) suggest that estuarine mortality is high (mean 45 %), and highly variable among years (22–59 %). However, these studies did not address any potential causes of the spatial or temporal variation in survival.

Our objectives were: 1) Evaluate temporal and spatial variation in survival during the outmigration to the ocean, 2) Evaluate the effect of flow and fork length on smolt survival, and 3) Determine whether there are differences in run timing, migration rate, estuary residence time, age composition, and parasite density between basins that may guide hypotheses to explain the mechanisms influencing differences in survival estimates between basins. In 2009, we directly compared the survival and behavior of wild steelhead smolts in the Nehalem and Alsea estuaries. To investigate the relationship between flow and survival we incorporated survival data from prior studies in the Nehalem [2001 and 2002 (Clements and Schreck 2003; Clements et al. 2011)] and Alsea 2007 (Johnson et al. 2010).

Methods

Study basins

The Nehalem River originates in Oregon’s Coast Range mountains and enters the Pacific Ocean near the town of Wheeler on the northern Oregon coast. The Nehalem River is approximately 192 km in length, draining a watershed of approximately 2,210 km^2. The North Fork Nehalem drains a watershed of 251 km^2. The estuary is defined as the area near the confluence of the North Fork Nehalem and the main stem of the Nehalem River. The estuary area that is accessible to fish at an average high tide is ~7.6 km^2.

The Alsea River originates in Oregon’s Coast Range mountains and enters the Pacific Ocean near the town of Waldport, near the middle of the Oregon coastline. The Alsea River, beginning at the confluence of the North and South Forks is 78 km in length and drains a watershed of 764 km^2. Fall Creek is a tributary that flows into the Alsea River at river kilometer (rkm) 50.4. The estuary is defined as the area below the Highway 34 bridge at Taylors Landing (Fig. 1). The estuary area that is accessible to fish at an average high tide is ~8.6 km^2.

Capture and tagging

In both basins, we collected wild steelhead smolts using a 1.5 m diameter rotary screw trap. The traps were located at river kilometer (rkm) 55 in the Alsea River and rkm 33 in the Nehalem River. The traps were checked in the morning and wild steelhead smolts were transferred to separate holding containers prior to tagging.

Each fish was anesthetized individually using tricaine methane sulfonate (50 mg/L MS-222 buffered with 125 mg/L $NaHCO_3$). The fish was then placed ventral side up in a wet foam wedge and dilute anesthetic (50 %) was perfused over the gills using a squeeze bottle. We made a 1–1.5 cm incision just anterior of the pelvic girdle and to the side of the mid-ventral line using a 5 mm micro-scalpel blade. The hydroacoustic transmitter was then inserted into the coelomic cavity, and the incision was closed using two sutures (simple interrupted) tied with two square knots. Following implantation, the fish were transferred to a recovery enclosure and placed in a slow moving pool downstream of the trap. The recovery enclosure consisted of a 2.5 cm tubular PVC frame encased with white fabric mesh (2.5×1.2×1 m, L×W×D). We observed the behavior of the fish in the enclosure to ensure they recovered normal body posture, gill ventilation, and avoidance behavior as we approached the enclosure (Clements and Schreck 2003). The fish were liberated at dusk of the same day to minimize predation and reduce holding stress. Survival during this period was 100 %. Previous research suggests that mortality from this procedure is 0–5 % (Schreck et al. 2002; Clements and Schreck 2003) after 1 month in a laboratory setting.

We used V7-2L acoustic tags (20 mm×7 mm, 1.6 g in air, 0.75 g in water) (AMIRIX Systems Inc., VEMCO Division-Halifax, Nova Scotia, Canada). Each transmitter was programmed with a random pulse rate of 15–30 s to minimize the risk of not detecting fast moving fish that passed within range of a receiver. The minimum expected tag life was 41 d. All tags were checked for acoustic transmission before implantation. Previous studies concluded that wild steelhead smolts in the Nehalem (Clements and Schreck 2003) and Alsea (Johnson et al. 2010) had mean travel times between tagging and ocean entry of 7 and 10 d respectively. All the fish tagged in the Nehalem had a tag to body weight ratio ≤5 %. In the Alsea, the tag to body weight ratio was <5 % for the majority (80 %) of fish, and between 5 % and 8 % for the remaining 20 % of fish.

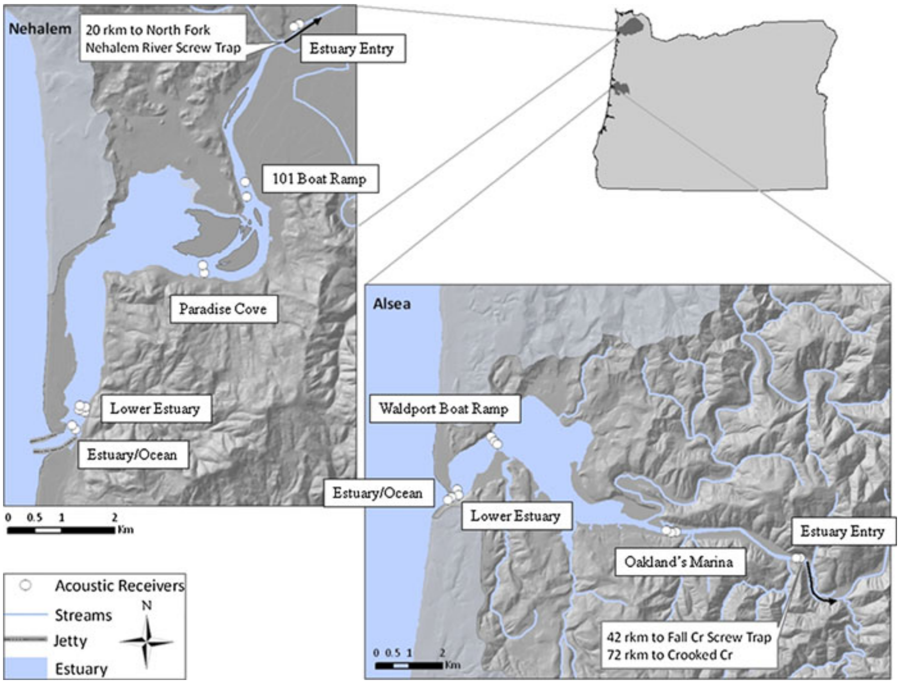

Fig. 1 Map of receiver array locations in the Nehalem and the Alsea estuaries in 2009. Upper right corner represents the outline of Oregon, located in the Northwest portion of the United States. Shaded areas highlight the two study basins. Enlarged sections illustrate the Nehalem and Alsea estuaries and receiver array placement within each estuary. Receivers are represented by circles, and "rkm" refers to river kilometer

To evaluate the temporal variability in survival throughout the emigration, we tagged fish during two time periods (early and peak) in each river system (Fig. 2). Early migrants (EM) or peak migrants (PM) were those that were tagged during the first portion of the run prior to the peak or those tagged at the peak, respectively. We defined the peak as a 2-week period when capture estimates were highest. The "late" group (LM), tagged in 2002, consists of smolts that were captured in the screw trap following the peak in outmigration.

During the early and peak periods, we tagged fish on at least 3 consecutive days to evaluate intra-period variation in survival. In the Nehalem, we tagged 35 smolts in the EM group (April 7–9th) and 34 in the PM group (April 20–22nd). In the Alsea, we tagged 21 smolts in the EM group between April 9–17th and 49 in the PM group between April 18–27th.

Monitoring survival and behavior

We monitored the passage of tagged fish using VR2 acoustic receivers (AMIRIX Systems Inc., VEMCO Division-Halifax, Nova Scotia, Canada). Receivers were placed in arrays at various points in the river, consistent with placement in 2001, 2002 (Clements and Schreck 2003), and 2007 (Johnson et al. 2010), to ensure migrating fish would pass within range of at least one receiver (Clements et al. 2005). Arrays were placed in the lower river between the screw trap and the estuary, in the upper estuary, mid-estuary, and lower estuary in as close proximity to the ocean as was practical, accounting for interference created by wave action, tidal currents, and personnel safety (Fig. 1). The receivers were downloaded weekly.

Parasite infection intensity and smolt condition

We euthanized a subsample of smolts on the days we tagged fish. The left side of the fish was filleted, and a portion of the posterior kidney was removed. The tissues were stored at −4 °C until processing. The remaining portion of the body was fixed in 10 % buffered formalin for histological evaluation.

Muscle and kidney samples were thawed and the entire amount of tissue weighed. We placed a subsample of muscle tissue (4.5–6.3 g) or the entire posterior kidney (0.02–0.24 g) between two pieces of Plexiglas with a small amount of water, and applied pressure to create a wet mount (Ferguson et al. 2010). We then examined the slide under a compound microscope to identify and enumerate parasites. Parasite density is defined as the average number of parasites per gram of tissue from only infected fish and prevalence is the number of fish infected divided by number sampled.

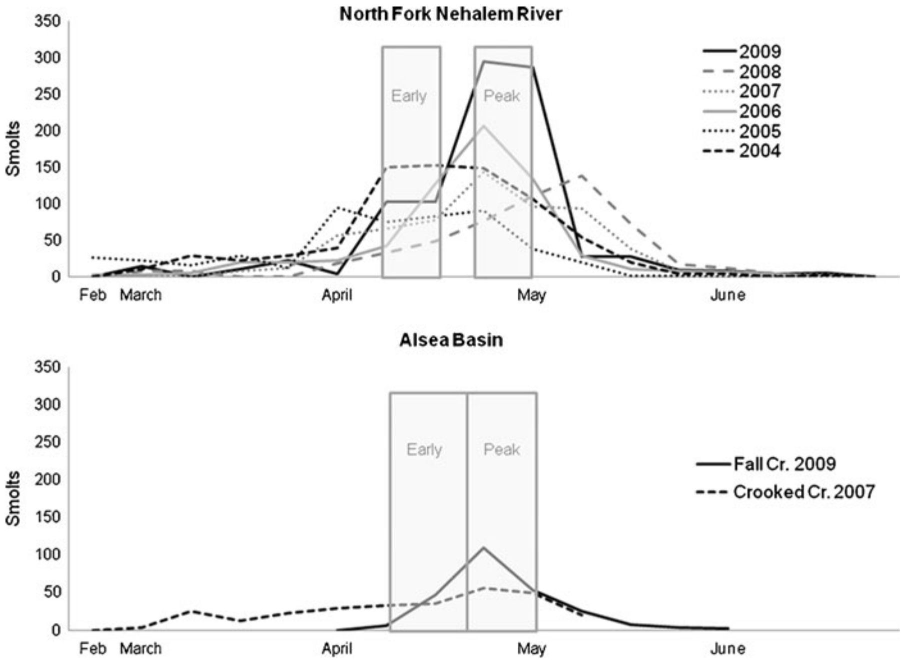

Fig. 2 Steelhead smolt outmigration timing from the North Fork Nehalem River 2004–2009 (ODFW Life Cyle Monitoring Project 2008), and the Alsea River. Crooked Creek and Fall Creek are tributaries of the Alsea River. *Gray boxes* indicate weeks when tagging took place during the 2009 field season

The remaining, fixed portion of the carcass was dissected for histology with sections of the following tissues removed: spleen, liver, ovary (if present), lower portion of intestine, heart, pyloric cecae, kidney, muscle, brain, and gill arches (decalcified in 15 % formic acid for 1 h before embedding). Slides were stained with hematoxylin and eosin using standard techniques.

We measured fork length (mm), recorded weight (g), and collected scale samples from all fish that were captured in the trap, including tagged fish and those that were euthanized for parasite analysis. Smolt scales were removed from the area between the dorsal and adipose fin, immediately dorsal of the lateral line on the left side. We determined the age by counting the number of annuli. Fulton's condition factor was calculated for all fish >120 mm using the formula $K = (\text{weight g})10^5 \Big/ (\text{fork length mm})^3$ (Carlander 1977).

Data analysis

Survival estimates

We used the single release-recapture Cormack-Jolly-Seber design (Cormack 1964; Jolly 1965; Seber 1965) in the Survival Under Proportional Hazards model to estimate survival and detection efficiency (Lady et al. 2009; SURPH 3.0 http://www.cbr.washington.edu/paramest/surph/). Survival estimates were calculated using detections at the lower estuary array located at rkm 1.2 in the Nehalem estuary and rkm 0.2 in the Alsea (Fig. 1). We estimated the efficiency of the lower estuary array using detections at the estuary/ocean transition array, which was in closest proximity to the ocean. Smolts last detected at the estuary/ocean array were assumed to be successful ocean entrants. There were instances when fish were detected at the estuary/ocean array, and later detected upstream at the lower estuary array then never detected again (0 fish in the Nehalem, 4 in the Alsea). Since the *last* detection for these fish was upstream of the last array these fish were not considered to be ocean entrants. In 2009, there was no array placed offshore in the Pacific Ocean. Therefore, the minimum number of tagged smolts entering the Pacific Ocean is presented based on detections at the estuary/ocean transition array. There are no standard errors associated with these numbers because there was no way to determine the efficiency of this last array.

Tags that were only detected one time at any given array were checked against available tag numbers and for legitimate time and date stamps within the context of the detections at other arrays and tidal cycles before they were considered viable detections.

Steelhead smolt survival in the estuary

We used logistic regression for binary response variables to assess the relationship between smolt survival in the estuary and fork length and basin. A total of 53 and 62 tagged smolts reached the Nehalem and Alsea estuaries, respectively. These 115 smolts were used for analysis of steelhead smolt survival in the estuary. The full model was: logit(survival) = intercept + fork length + basin + (fork length × basin). The interaction term between basin and fork length was included to incorporate the possibility that the relationship between length and survival differed in the two river basins. We used the drop in deviance F-test to compare competing models to test the importance of individual parameters within the model. We used a pooled variance, two sample *t*-test to compare differences in the initial fork length (measured at time of tagging) between fish that were detected entering the estuary and those that were not, to test for size selective mortality. We used S+ 8.0 (Insightful Corp., Seattle, Washington, USA) for all statistical analyses. A p-value ≤ 0.05 was considered significant.

Using data from prior years [Nehalem 2001 and 2002 (Clements et al. 2011), Alsea 2007 (Johnson et al. 2010)] and our current study, we evaluated the relationship between river flow and smolt survival using logistic regression with binary response variables. The fish in the Nehalem River were all tagged at the same site and passage was monitored at the same sites in the estuary. The site of tagging differed between years in the Alsea River (by 28 km), but fish passage in the estuary was monitored at the same sites in both years. All of the fish tagged on the same date were assigned to a single group. Fish tagged after June 1 were omitted from this analysis, including nine fish from 2001, and three fish from 2002 in the Nehalem basin because of suspected residualization (Clements et al. 2011). Using the release date and the time of first detection in the estuary for each fish that was detected, we were able to calculate the average time spent in the river for fish within each group. Then, we calculated average daily flow (m^3/sec) for that time period, beginning the day following the release date because tagged fish were released at dusk. Daily river discharge data were provided by U.S. Geological Survey gauging stations 14301000 on the Nehalem River near Foss, OR and 14306500 Alsea River near Tidewater, OR (USGS real-time water data http://waterdata.usgs.gov/nwis/). The full model was: logit(survival) = intercept + flow + year + basin + (flow × year) + (flow × basin) + (year × basin) + (flow × basin × year). Interaction terms were included to incorporate the possibility that the relationship between flow and survival differed within each basin, between basins, or between basins within the same year.

Steelhead smolt behavior

We evaluated the relationship between migration timing and estuary residence time between basins and between early and peak groups using an exact Wilcoxon rank-sum test. We calculated the time each fish spent in the estuary (estuarine residence time) using the time elapsed between the last detection at the estuary entry array and the last detection at the lower estuary array.

Parasite infection intensity and smolt condition

We compared the density of *N. salmincola* in the posterior kidney between fish from each basin, and among fish of different age groups. We used an exact Wilcoxon rank-sum test to compare *N. salmincola* densities between 1 and 2 year old fish from the Alsea River, and a Kruskal-Wallis rank sum test to compare densities among 1, 2, and 3 year old juveniles from the Nehalem River. The densities of *N. salmincola* were high and prevalence was 100 %, making this species the most appropriate parasite for analysis (larger sample size).

Results

Survival

The estimated survival of tagged fish to the ocean was 49 % (SE 6 %) in the Nehalem and 59 % (SE 7 %) in the Alsea (Table 2). The mortality for each zone was generally inversely related to the distance from the ocean (Fig. 3). Survival was variable among releases;

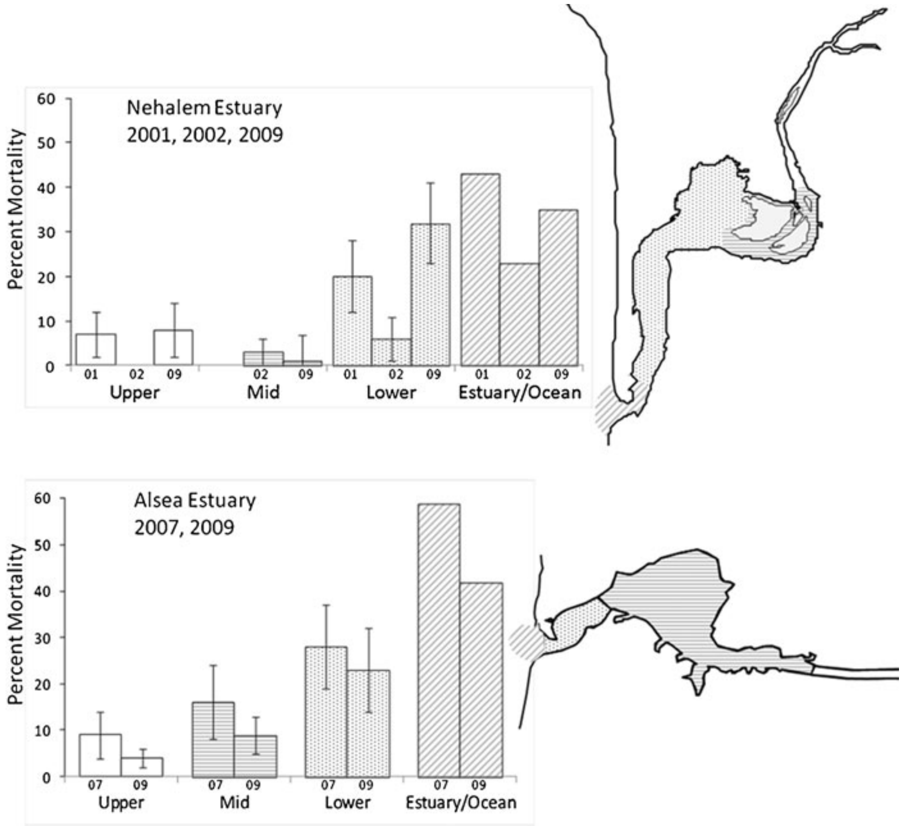

Fig. 3 Percent mortality for each estuary zone (Upper, Mid, Lower, Estuary/Ocean) in the Nehalem (2001, 2002, 2009) and Alsea (2007, 2009) estuaries. *Bars* represent the percent of undetected fish (percent mortality) within each zone and standard error. The estuary/ocean transition zone has no standard error bars because estimates for efficiency of the last array were not possible. Estuary outlines are not proportional to actual size differences between estuaries, and are for representation of zones only

however, survival probability was generally higher for fish tagged and released during the peak of the migration than those tagged in the early portion of the outmigration (Table 3). The detection efficiency was high (>90 %) in almost all cases (Table 1) with the exception of the Paradise Cove array in the Nehalem estuary (88 %), and the lower estuary array in the Alsea estuary (82 %).

Effect of size and environment on survival

We were only able to directly compare annual survival between basins in 2009. We found no effect of fork length $\left[\Pr\left(\chi_1^2 > 1.777\right) = 0.183\right]$, river basin $\left[\Pr\left(\chi_1^2 > 0.668\right) = 0.414\right]$, or the interaction between these two variables $\left[\Pr\left(\chi_1^2 > 0.438\right) = 0.508\right]$ on survival in 2009. Smolts tagged in the North Fork Nehalem (mean length: 175 mm, 95 % CI: 171–178 mm) were larger than those tagged in the Alsea (mean length: 160 mm, 95 % CI: 156–164 mm; t_{134}=−5.60, p<0.0001). The mean fork length of smolts at the time of tagging which subsequently entered the estuary was 175 mm (95 % CI: 168–182 mm) in the Nehalem, and 162 mm (95 % CI: 143–181 mm) in the Alsea, suggesting that smaller fish did not die or lose tags at a higher rate between tagging and entry to the estuary. Of the 14 fish tagged in the Alsea that had a tag to body weight ratio between 5 % and 8 %, nine were detected at the lower estuary array.

We evaluated the effect of flow on survival using logistic regression. The three-way interaction term (basin×year×flow) was significant (p=0.01) in the full model. Therefore, we used a separate logistic regression model for each combination of basin and year. The final model used for analysis of each year and basin combination was logit (survival) = intercept + flow. We observed no significant relationship between flow and survival in the Alsea basin in 2007, or the Nehalem basin in 2001 (Table 4). In contrast, we did observe a negative relationship between flow and survival in the Alsea basin in 2009 and the Nehalem basin in 2002 and 2009 (Table 4), suggesting that increased flow was associated with decreased survival in tagged fish.

Behavior

The median travel time from the smolt trap to the first detection at the lower estuary array in the Nehalem basin (33 km) was 10.0 d for the EM group (n=13, range 4.4–24.6) and 7.8 d for the PM group (n=21, range 4.7–12.6). In the Alsea basin the median migration time from smolt trap to the lower estuary array (55 km) was 20.4 d for EM (n=10, range 15.0–42.9) and 13.0 d for the PM (n=28, 6.1–33.2).

We estimated the rate of migration for the peak and early groups based on the difference in time between tagging to the time of first detection at the lower estuary array. Fish from the PM group tended

Table 1 Receiver efficiencies and associated standard errors (SE) reported using SURPH 3.0 survival model. NA indicates that no receiver array was present at this location for the corresponding year

Nehalem River		Receiver array efficiency (SE)		
Location	River kilometer	2001	2002	2009
Estuary entry	13.5	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)
Hwy 101 boat ramp	9.7	NA	1.00 (0.00)	0.93 (0.04)
Paradise cove	6.8	1.00 (0.00)	0.94 (0.04)	0.88 (0.06)
Lower estuary	1.2	1.00 (0.00)	0.96 (0.04)	1.00 (0.00)

Alsea River		Receiver array efficiency (SE)	
Location	River kilometer	2007	2009
Fall Creek confluence	50.4	1.00 (0.00)	0.98 (0.02)
Head of tide	23.7	1.00 (0.00)	1.00 (0.00)
Estuary entry	13.0	1.00 (0.00)	1.00 (0.00)
Oakland's Marina	9.0	0.90 (0.05)	1.00 (0.00)
Waldport boat ramp	2.6	0.86 (0.07)	0.95 (0.04)
Lower estuary	0.2	0.91 (0.90)	0.82 (0.08)

to move faster in the Nehalem than those from the EM group, but the difference was not significant (W=197, p=0.066). The median migration rate was 3.2 km/d (n=13, range 1.1–7.6 km/day) for the EM group, and 4.2 km/d (n=21, range 2.6–7.0) for the PM group. In the Alsea basin, the median migration rate was faster for PM (4.2 km/d, n=28, range 1.7–9.1 km/d) than EM (2.7 km/d, n=10, range 1.3–3.7 km/d) (W=117, p=0.0086). There was no difference in migration rate between basins after the fish from the EM and PM groups were pooled (W=1,364, p=0.649).

The median estuarine residence time for smolts in the Nehalem estuary was 0.72 d (n=34, range 0.14–7.9) and 0.83 d (n=38, range 0.14–6.3) in the Alsea Estuary. There was no difference in residence time between fish in the EM (n=13) and PM (n=21) group in the Nehalem basin (W=266, p=0.181), nor did residence time differ between fish in the EM (n=10) and PM (n=28) groups in the Alsea basin (W=160, p=0.257). In addition, there was no difference in residence time between basins (W=1,327 Alsea n=38, Nehalem n=34, p=0.504).

Age, parasite infection intensity and smolt condition

In 2009, the outmigrants from the Nehalem basin consisted of 1 (18 %), 2 (74 %), and 3 (8 %) year old smolts (n=119). In contrast, 46 % of the outmigrants in the Alsea basin were 1 year olds, and 54 % were 2 year olds (n=98). There were no 3 year olds captured from the Alsea basin.

We identified several species of parasites in fish captured in the Alsea basin. These included: *N. salmincola* in the brain, heart, gills, muscle, anterior kidney, posterior kidney, pyloric cecae and intestines; *Sanguinicola* sp. in the gills; *Chloromyxum majori* in the anterior kidney; *Myxidium salvelini* in the anterior kidney; *Myxobolus* sp. in the muscle and brain tissue; adult digenean trematodes in the pyloric cecae and intestine; and *Salmincola* sp. were found externally behind the pectoral fins and on the gills. These species were also identified in fish from the North Fork Nehalem River in corresponding tissues. In addition, we also found *Echinochasmus milvi* in the gill; *Ceratomyxa shasta* in the intestine; *Apophallus* sp. in the muscle; and *Philonema* sp. in the coelomic cavity from smolts in the Nehalem River. Selected parasites, their prevalence and density are illustrated in Table 5.

The density of *N. salmincola* in the posterior kidney was higher (exact Wilcoxon rank-sum W=239, p<0.0001) in fish from the Nehalem River (n=24; median=13,454; range 2,614–30,673) than in the Alsea (n=20; median=2,792; range 150–12,050). There was no difference in the density of *N. salmincola* in the posterior kidney among the three age groups in the Nehalem (Kruskal-Wallis $\chi^2_2 = 4.297$, p=0.12), nor did *N. salmincola* density differ between 1 and 2 year old juveniles from the Alsea River (exact Wilcoxon rank-sum W=82, p=0.09). The average sample weight for posterior kidney samples was 0.10 g (n=44, range 0.02–0.24). The condition factor for fish >120 mm in the Nehalem was lower than in the Alsea River (Wilcoxon rank-sum Z=8.38, p<0.0001). The median condition factor for fish in the Nehalem River was 0.93 (n=144, range 0.80–1.1), and 1.03 (n=124, range 0.84–1.3) in the Alsea River.

Discussion

Steelhead smolt survival and behavior

Smolt survival to the ocean is currently estimated using data collected from smolt traps located well upstream of the estuary. Thus, any mortality incurred in the zone between these traps and the ocean is included as ocean mortality in survival models (Jepsen et al. 2006). Our data suggest that 50 % or more of the mortality previously considered as ocean mortality actually occurs in the estuary.

The fish we tagged were generally representative of the entire size range of fish captured at the smolt traps (Fig. 4). Furthermore, both in our study and prior studies (Johnson et al. 2010; Clements et al. 2011), the majority of tagged steelhead migrated successfully to the estuary following release (range 63–89 %). After smolts entered the estuary survival tended to decrease as the smolts neared the ocean (Fig. 3). A large proportion of the outmigrating fish were not detected entering the ocean after successfully migrating to the lower estuary, a distance of 1–1.5 km (mean loss: 59.4 % over the five studies).

In 2001 and 2002 Clements et al. (2011) placed two lines of receivers in the ocean ~1.0 km offshore of the Nehalem estuary. Using these arrays the authors demonstrated that the ocean array was relatively efficient at detecting fish passage, 62.5 % and 83 % in 2001 and 2002, respectively. After adjusting the survival

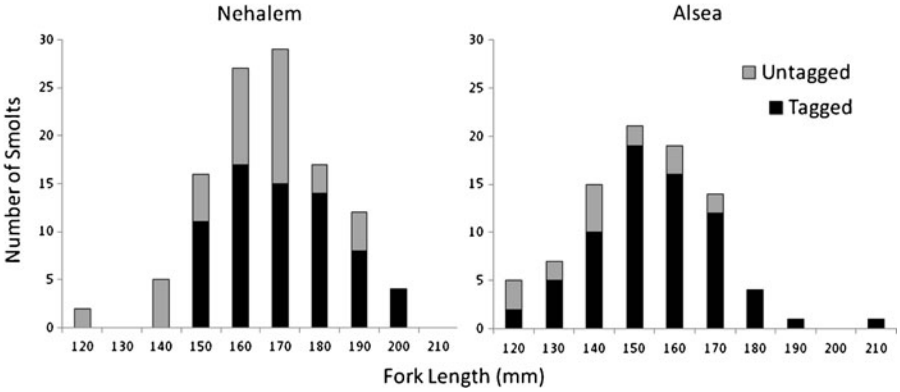

Fig. 4 Distribution of fork length (mm) of wild steelhead smolts captured in the Nehalem and Alsea basins in 2009

estimates using these efficiencies, the survival probability remained low in the section between the lower estuary and the ocean. This illustrates that the decreased survival estimates in the lower region of the estuary are likely not due to lower receiver efficiency.

Predation has already been identified as one of the primary factors for smolt mortality in these estuaries (Stahl et al. 2000; Schreck et al. 2002, 2006; Clements et al. 2011). Large numbers of predators congregate near the mouth of each of these rivers (Clements and Schreck 2003; Wright et al. 2007) and the transition from fresh water to marine environments is a critical stage in the life history of anadromous salmonids (Levings 1994). Therefore, it is not unreasonable to expect that mortality may be high in the lower estuary. However, our estimates of survival to ocean entry in this study are a minimum, actual survival is likely higher due to a number of factors including possible missed detections, tag shedding, residualization of tagged fish in the river, and mortality due to surgery complications.

A number of studies have shown that larger smolts survive at a higher rate to adulthood (Wagner 1967; Ward and Slaney 1988). However, there was no effect of fork length on survival in the estuary, which is consistent with other studies (Johnson et al. 2010; Moore et al. 2010). Using a 17 year dataset for coho salmon, Holtby et al. (1990) noted that smolt size in coho salmon was not consistently related to smolt to adult survival, but that large smolts did survive better in the ocean when marine survival was relatively poor. Taken together, these observations suggest that size selective mortality of smaller smolts may occur primarily in the marine environment.

Our estimates of survival are higher than those reported by researchers working in much larger estuarine environments. Melnychuk et al. (2007) reported conservative survival estimates for steelhead smolts leaving the Cheakamus River, British Columbia of 27 % during 2004 and 2005. Similarly, Moore et al. (2010) reported combined survival from populations in four separate rivers through Puget Sound and into the Strait of Juan de Fuca as 28.3 %. Such low survival likely reflects the distance traveled within the estuarine environment, as suggested by Melnychuk et al. (2007). In both of these studies, steelhead smolts travelled 155–230 km, depending on release site and route travelled. Estuarine residence time is also thought to be inversely proportional to the probability of survival to the ocean (Handeland et al. 1996; Clements and Schreck 2003; Schreck et al. 2006; Truelove 2006; Kennedy et al. 2007). In contrast, wild steelhead smolts spent ~1 d in the estuary according to all five of our data sets and incurred approximately 50 % mortality. Regardless of estuary size and residence time, estuarine survival appears to be low during most years. However, we cannot say whether these mortality rates are outside of the historic range because there is no historic data available.

Inter annual variation

The estimates of survival were highly variable among years, and ranged from 49 % to 78 % in the Nehalem for the 3 years (2001, 2002, 2009), and from 41 % to 59 % in the Alsea for the 2 years (2007, 2009) (Table 2). Furthermore, we observed considerable variation in survival between groups tagged on consecutive days (data not shown). With increased monitoring of smolt survival through the estuary researchers may be able to determine which environmental factors have the greatest impact on survival and better inform efforts to increase smolt survival to the ocean (Tables 3, 4 and 5).

Environmental cues that initiate smoltification are numerous and complex. McCormick et al. (1998)

Table 2 Number of smolts tagged each year and survival probability estimates between arrays based on SURPH 3.0 results. Standard errors (SE) for the estimates are in parentheses. Standard errors are not presented for estuary/ocean arrays because there is no array behind them with which we could estimate efficiency. "NA" indicates that no receiver array was present at this location for the corresponding year. "Rkm" refers to the river kilometer where each array was located. Overall survival estimates are calculated from point of tagging to the lower estuary arrays. Minimum survival is based on the number of fish detected at the estuary/ocean transition array

Nehalem River	Survival Probability (SE)			Rkm
	2001	2002	2009	
Number Tagged	56	45	69	
Trap - Estuary Entry	0.63 (0.06)	0.84 (0.05)	0.77 (0.05)	33.2 - 13.5
Upper Estuary	NA	1.00 (0.00)	0.85 (0.05)	13.5 - 9.7
Mid Estuary	0.94 (0.04)	0.98 (0.03)	0.98 (0.04)	9.7 - 6.8
Lower Estuary	0.85 (0.06)	0.95 (0.04)	0.77 (0.07)	6.8 - 1.2
Estuary/Ocean	0.59	0.77	0.64	1.2 - 1.0
Overall Survival	0.50 (0.07)	0.78 (0.06)	0.49 (0.06)	
Minimum Survival	0.29	0.60	0.32	

Alsea River	Survival Probability (SE)		Rkm
	2007	2009	
Number Tagged	72	70	
North Fork Alsea - Fall Creek Confluence	0.79 (0.05)	NA	83.4 - 50.4
Fall Creek Trap - Fall Creek Confluence	NA	0.97 (0.02)	55.0 - 50.4
Fall Creek - 5-Rivers	0.98 (0.02)	0.96 (0.03)	50.4 - 39.8
5-Rivers - Head of Tide	0.95 (0.03)	0.98 (0.02)	39.8 - 23.7
Head of Tide - Estuary Entry	1.00 (0.00)	0.97 (0.02)	23.7 - 13.0
Upper Estuary	0.93 (0.04)	0.97 (0.02)	13.0 - 9.0
Mid Estuary	0.83 (0.07)	0.90 (0.04)	9.0 - 2.6
Lower Estuary	0.73 (0.09)	0.77 (0.08)	2.6 - 0.2
Estuary/Ocean	0.39	0.58	0.2 - 0.1
Overall Survival	0.41 (0.07)	0.59 (0.07)	
Minimum Survival	0.15	0.31	

Table 3 Survival probability and standard error (SE) for wild steelhead smolts tagged in different groups (early, peak, late) throughout the run

	Early (n)	Probability of survival (SE)	Peak (n)	Probability of survival (SE)	Late (n)	Probability of survival (SE)
Nehalem						
2001	19	0.58 (0.11)	19	0.63 (0.11)	18	0.28 (0.11)
2002	4	0.67 (0.14)	28	0.76 (0.10)	13	0.92 (0.07)
2009	35	0.37 (0.08)	34	0.62 (0.08)		
Alsea						
2007	72	0.41 (0.07)				
2009	21	0.51 (0.13)	49	0.63 (0.09)		

proposed the concept of an “ecological smolt window”, a period in which smolts have evolved to emigrate triggered by environmental factors at times optimal to their survival. The consistent, relatively high survival rate that we observed for fish migrating during the peak (>60 %) may be partially explained by this phenomenon. In addition, outmigration as part of a larger aggregation may offer survival benefits. Schooling fish are thought to be more efficient at capturing food and are less susceptible to predation than those that remain solitary (Pitcher 1986). Smolts migrating at the peak of the run could potentially realize higher survival as they would already be traveling in a large group, beginning to exhibit schooling behavior prior to ocean entry.

There may also be a ‘dilution’ in predation pressure provided by release of hatchery smolts that are less well adapted to natural ecological factors. Hatcheries were constructed in both of our study basins in the early 1900’s and support large winter steelhead fisheries that target supplemental hatchery fish. Volitional release of smolts in both basins begins in early April, overlapping with the observed wild smolt run timing (ODFW North Nehalem operations plan 2009; ODFW North Fork Alsea River Hatchery operations plan 2009). Our tagged fish were reared in their natal streams, however, we cannot rule out the possibility of prior genetic influence from hatchery fish (Jepsen et al. 2006; Johnson et al. 2010). We recognize the possibility that contributions from hatchery reared parents and hatchery smolt releases could be variables that influence behavior and survival within and among years but these effects were not the focus of this study.

Increased river flow has been associated with an increase in smolt survival (Kjelson and Brandes 1989; Conner et al. 2003) and is thought to be due to increased turbidity, which decreases the effectiveness of predators (Gregory 1993; Gregory and Levings 1998; Emmett 2006; Emmett and Sampson 2007). These studies were conducted in large river systems like the Sacramento, Snake, Columbia, and Fraser rivers which may not be comparable to our study area. The Snake, Columbia and Sacramento rivers contain multiple dam impoundments that greatly alter river flow and temperature from their natural condition. In contrast, in smaller unimpounded coastal systems like in our study we found that steelhead smolt survival decreased with increased flow in three of our five datasets (Alsea 2009, Nehalem 2002, 2009). There was little variation in flow throughout the outmigration in the Alsea basin in 2007 season, so we would not expect to see a relationship between flow and survival in this instance.

An inverse relationship between flow and survival is difficult to explain. We speculate that it may relate to a decreased ability to detect and avoid predators due to increased turbidity (Gregory 1993). Both estuaries

Table 4 Logistic regressions for the effect of flow on survival. *P*-values reported are two-tailed, asterisks identify significant *p*-values; N is the number of tagged fish used for the analysis

Basin	Year	N	Coefficient	SE	P
Alsea	2007	72	−0.078	0.167	0.646
Alsea	2009	70	−0.0813	0.035	0.019*
Nehalem	2001	47	0.016	0.023	0.478
Nehalem	2002	42	−0.0431	0.018	0.015*
Nehalem	2009	69	−0.0235	0.010	0.022*

Table 5 Parasite prevalence and density of select parasites in selected tissues from the Nehalem and Alsea basins organized by smolt age class

	Kidney[a]	Muscle[a]		Gill			Brain		Heart
	Nano	Nano	Apo	Nano	Echino	S. cola	myxo	Nano	Nano
	Prevalence								
Nehalem									
Age 1	100 %	100 %	100 %	100 %	100 %	75 %	25 %	0 %	50 %
Age 2	100 %	100 %	92 %	100 %	46 %	85 %	46 %	0 %	92 %
Age 3	100 %	100 %	71 %	100 %	86 %	100 %	71 %	14 %	100 %
Alsea									
Age 1	100 %	100 %	0 %	80 %	0 %	80 %	50 %	0 %	60 %
Age 2	100 %	100 %	0 %	80 %	0 %	90 %	20 %	20 %	60 %
	Density (Range)								
Nehalem									
Age 1 (*N*=4)	8,020 (3,450–13,450)	41 (4–72)	3 (1–6)	14 (1–14)	5 (1–12)	34 (5–57)	8 (8)	0	6 (3–8)
Age 2 (*N*=13)	14,710 (2,614–25,215)	49 (2–87)	4 (1–18)	20 (1–76)	7 (2–17)	86 (3–346)	12 (1–47)	0	10 (1–35)
Age 3 (*N*=7)	16,692 (7,163–30,673)	34 (10–66)	6 (1–18)	32 (7–56)	13 (1–34)	136 (7–374)	9 (2–21)	1 (1)	9 (4–19)
Alsea									
Age 1 (*N*=10)	2,736 (150–12,050)	11 (2–25)	0	4 (1–12)	0	53 (2–212)	24 (3–69)	0	2 (1–5)
Age 2 (*N*=10)	3,918 (636–7,807)	9[b] (5–17)	0[b]	5 (2–11)	0	20 (2–73)	5 (4–6)	1 (1)	2 (1–5)

Nano=*Nanophyetus salmincola*, *Apo*=*Apophallus* sp., *Echino*=*Echinochasmus milvi*, *S.cola*=*Sanguinicola* sp., *myxo*=*Myxobolus* sp.

[a] Data from muscle and kidney were derived by wet mount, which were standardized to number of parasites per gram of tissue. Data from all other tissues are from histology and are presented in terms of parasites per histological sections. Data for gill parasites are based on three gill arches per fish

[b] For these data *n*=9, and no muscle sample was available for one fish in this group

support large numbers of double crested cormorants (*Phalacrocorax auritus*) and harbor seals (*Phoca vitulina*). Harbor seals have been documented feeding in low light conditions on the Puntledge River in British Columbia, Canada. In the Puntledge River seals were observed "positioned parallel to one another, ventral side up to form a feeding line across the river to intercept thousands of outmigrating salmonid smolts" at night, using illumination provided by lights from two bridges crossing the river (Yurk and Trites 2000). There is little research on the factors affecting foraging efficiency of these species, but it is conceivable that they are able to continue foraging in more turbid waters by congregating at natural prey funnels created by shallow water, or very narrow sections of the estuary.

Parasite prevalence and infection intensity

We observed a significant difference in parasite load between smolts collected in the Alsea and Nehalem basins. Many of the smolts that were outmigrating from the North Fork Nehalem had a high parasite load, especially *N. salmincola*. If survival estimates for smolts emigrating from the Nehalem estuary had been markedly lower than for those in the Alsea, we would have suspected that parasite load between basins was a contributing factor to smolt mortality in the estuary. Because the smolts used for parasite analysis were lethally sampled we have no direct link to the influence of these parasites on survival through the estuary. However, these results are relevant in the context of documenting factors that may affect smolt to adult survival. *N. salmincola* can cause death of the host (Baldwin et al. 1967), are negatively associated with various performance endpoints in juvenile coho salmon (Ferguson et al. 2012), and have been linked to parasite associated mortality during early ocean residence of juvenile coho salmon (Jacobson et al. 2008). Metacercariae of *N. salmincola* remain viable in coho salmon for at least 33.5 months, including their stay in the ocean (Farrell et al. 1964).

In this study, we used acoustic telemetry to quantify the behavior and survival of juvenile *O.mykiss* in small estuaries. In addition, we used a multidisciplinary approach to provide baseline data on a variety of variables known to affect smolt survival. Our results highlight the importance of estimating survival in the estuary to improve the spatial resolution of survival models. Historically, at least 50 % of the mortality that has previously been included in survival models as 'ocean mortality' may be assigned to the estuary. By assigning mortality to where it actually occurs we will be better equipped to investigate how environmental variables affect smolt survival. Monitoring estuary smolt survival would be beneficial for measuring success of restoration projects or the impact of predator control programs if such actions were put in place to improve smolt survival. Steelhead smolts do not currently appear to spend much time in the estuaries in our study basins, but we do not know if that was the case historically. Information regarding smolt behavior, parasites and disease, and environmental factors that influence smolt survival between basins within the same distinct population segment contribute to the understanding of the complexities involved in the management of anadromous salmonids, and could be used to direct future research. Once smolts reach the ocean we have little opportunity to influence their survival.

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