Habitat-mediated effects of diurnal and seasonal migration strategies on juvenile salmon survival

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Behavioral decisions during periods of vulnerability to predation risk, such as migrations during the juvenile life-history stage, may strongly affect the probability of survival. Habitats through which animals migrate are heterogeneous, and risk-reducing behaviors may be more important in some habitats than others. Using biotelemetry data, diurnal and seasonal riverine migration patterns of \textgreater3800 juvenile salmon across 4 species, 12 watersheds, and 5 years were quantified to evaluate possible effects of migration timing on survival from lower river reaches to coastal waters. In small, clear rivers most salmon avoided migrating during daylight hours and average survival of fish migrating at night (55%; 95% confidence limits 50--61%) was twice that of fish migrating in daylight (24%; CL 17--31%). Conversely, in the large, heavily silted Fraser River neither preference for nocturnal travel nor effects of diurnal timing on survival were observed. Early ocean survival was also influenced by the timing of ocean entry, but in opposite directions for fish from the Fraser River and smaller rivers. In the Fraser River, average survival for later migrants (69%; CL 60--77%) was nearly twice that of earlier migrants (38%; CL 33--44%), likely related to seasonal increases in river flow. In contrast, in smaller rivers, average survival for earlier migrants (70%; CL 65--74%) was 3-fold greater than survival for later migrants (19%; 95% CL 14--25%). Together, these results demonstrate that timing decisions affecting survival of juvenile salmon during their migration are likely mediated by landscape characteristics that plausibly influence the risk of predation.

Key words: animal migration, diel patterns, illuminance, mortality, Oncorhynchus, visual predators.

INTRODUCTION

Behavioral decisions by animals may affect the chance of survival (Lima and Dill 1990; Smith and McWilliams 2014; Hertel et al. 2017), with juvenile stages typically suffering high and variable mortality rates (Lorenzen 1996) that result in high selection pressures. In particular, periods of migration are physically challenging, often exposing individuals to elevated levels of predation risk (Baker 1978; Alerstam et al. 2003; Smith and McWilliams 2014). For species with a juvenile migration period, migrating individuals must make timing choices at both daily and seasonal scales, and behaviors that reduce predation risk are likely to be strongly selected (Lima and Dill 1990).

Habitats are not homogenous. Populations often occupy or travel through a diversity of habitats (Gregory and Levings 1998; Bradford and Higgins 2001) wherein selection pressures are shaped by local environments. The characteristics of one habitat may shift life-history strategy trade-offs in one direction, while characteristics of a different habitat may shift them in another, presumably necessitating different behaviors to maximize lifetime survival in the face of these trade-offs (e.g., Metcalfe et al. 1998; Railback et al. 2005). In salmonid fishes, the smolt is the life-history stage that migrates from natal freshwater habitats to marine waters. After smoltification (the period of physiological adjustment for saltwater tolerance) is complete, entering the ocean relatively early may allow individuals to take advantage of seasonal zooplankton availability which follow spring phytoplankton blooms (Healey 1980; Bilton et al. 1982; Scheuerr et al. 2009), although arriving too early may precipitate periods of high zooplankton abundance. On the other hand, constant travel downstream and through estuaries may expose smolts to visual predation risk (Mann 1982; Mace 1983; Greenstreet et al. 1993), so reducing exposure by restricting periods of active travel to nighttime may be advantageous (Metcalfe et al. 1998; Railback et al. 2005), even if that delays the time of
ocean entry. Any preference for nocturnal travel that may exist might also change during the migration season (Moore et al. 1995; Ibbotson et al. 2006), as delaying ocean entry too long could reduce opportunities for high growth rates in marine waters (Beamish and Mahnken 2001).

Consequences of diurnal migration timing strategies may vary among habitats through which juvenile salmon migrate. Small coastal rivers in British Columbia (BC) typically have clear water through which smolts can be easily seen by predators (Mace 1983; Wood 1997; Beamish et al. 1992; Furey et al. 2013; Furey et al. 2016) while the much larger Fraser River has greater flow and large sections drain regions of ice age loess deposits in the interior of the province. This results in much higher silt loads, which make smolts far less vulnerable to visual predation risk (Gregory and Levings 1998; Chase et al. 2013; Spence and Dick 2014). Avoiding visual exposure during daylight hours by restricting travel to nighttime may therefore be beneficial to juvenile fish in smaller rivers, but less important in larger rivers or coastal waters.

In this study, we evaluate effects of salmon migration timing strategies on survival from rivers to coastal waters. We address 3 hypotheses:

1. Deleterious survival consequences of migrating during daylight hours will be greater in clear rivers than in silted rivers as a result of greater visual predation risk in clear rivers.
2. In vulnerable habitats (small, clear rivers) salmon smolts will time their downstream and estuarine migration so as to reduce movements and thus exposure to visual predation risk during daylight hours, whereas in less vulnerable habitats (fast, silty rivers, and marine waters), preference for nocturnal travel will be less pronounced.
3. Smolts migrating downstream later in the season will be less selective with respect to diurnal travel preferences, because delaying their timing of ocean entry even further may have consequences for reduced marine growth.

**METHODS**

The Pacific Ocean Shelf Tracking Project (POST), one portion of the Ocean Tracking Network, is a large-scale acoustic telemetry array on the west coast of North America. The portion in southern BC (Welch et al. 2011) involves acoustic receivers placed in lower reaches of rivers and coastal waters of the Strait of Georgia ecosystem (Figure 1). Under POST, 3812 salmon smolts from 12 watersheds in southern BC had acoustic transmitters (VEMCO V7 or V9 tags) surgically implanted prior to migrating downstream (Welch et al. 2011). Acoustic receivers were deployed near river mouths and across the coastal Straits of Georgia (NSOG), Queen Charlotte (QCS), and Juan de Fuca (JDF) to detect tagged salmon that migrated past (Figure 1). Smolts of 4 species (coho salmon *Oncorhynchus kisutch*, steelhead *O. mykiss*, sockeye salmon *O. nerka*, and Chinook salmon *O. tshawytscha*) and 2 rearing histories (wild or hatchery-reared) were released in fresh water across 5 years of study (2004–2008), with 7 release sites in Fraser River tributaries and 10 sites in smaller rivers (Welch et al. 2011).

Surgical methods used to implant acoustic tags into salmon smolts have been published previously (Welch et al. 2007; Chittenden et al. 2009; Rechisky and Welch 2010; Collins et al.

![Figure 1](https://academic.oup.com/beheco/article-abstract/29/6/1340/5090112/1340)  
**Figure 1**  
Map of study area. Red circles show acoustic receiver locations. Ocean receivers were in place for years 2004–2008 at Queen Charlotte Strait (QCS), northern Strait of Georgia (NSOG), and Juan de Fuca Strait (JDF). Receivers were also in place in lower river reaches or estuaries to detect outmigrating salmon smolts. Blue ‘×’ symbols show release locations of tagged salmon, in the Fraser watershed (A–Coldwater River hatchery, B–Coldwater River rotary screw trap, C–Nicola River hatchery, D–Spius Creek hatchery (downstream), E–Spius Creek hatchery (upstream), F–Deadman River rotary screw trap, G–Sweltzer Creek (Cultus Lake hatchery)), and in smaller rivers (H–Seymour River hatchery, I–Cheakamus River (upstream), J–Tenderfoot Creek hatchery, K–Cheakamus River wild and hatchery (downstream), M–Cowichan River hatchery, N–Englishman River rotary screw trap, O–Nimpkish River rotary screw trap and Gwa’ni Hatchery, P–Nimpkish River (Woss Hatchery), Q–Keogh River fish fence).
2013; Morrison et al. 2013). Briefly, a tag was inserted into the abdominal cavity through a mid-ventral line incision, which was closed using 1–3 polydioxanone monofilament sutures. Gills were continuously irrigated during surgery with recirculating water, continually monitoring temperature and dissolved oxygen levels. Analgesics and anesthetics were used to minimize stress or pain in the animal subjects. After surgery, fish were transferred to a recovery tank and were generally held for ≥2 days after survey to monitor levels of tagging-related mortality, tag extrusions, and signs of impaired swimming behavior. Across all tagged fish, approximately 95% of smolts were within a recommended threshold of length_{tag}/length_{smolt} ratio of 0.16 (Lacroix et al. 2004), tagging-related mortality was observed in 0.7% of tagged smolts, and a single tag was extruded prior to releasing fish. Supporting laboratory studies (Welch et al. 2007; Chittenden et al. 2009; Rechisky and Welch 2010; Collins et al. 2013; Morrison et al. 2013) generally showed some initial short-term reduction in growth of surgical-tagged fish relative to control groups, but this was transient, with tagged animals resuming normal growth rates within a few weeks. The surgical tagging and handling procedures used for all animals in this paper were annually reviewed and approved by Fisheries & Oceans Canada, Pacific Region Animal Care Committee (Approvals #04-025, #04-026, #05-004) or the Vancouver Island University Animal Care Committee (Approvals #2006-08R-1, #2006-08R-2). Approved animal care applications included descriptions of how animals were to be treated ethically, field handling procedures, and justifications for the sample sizes employed. Sample sizes for all release groups are shown in Table 1, and body lengths, release dates, and tag sizes used for these release groups are provided in Supplementary Material 1.

Migration patterns of juvenile salmon were quantified to identify possible behavioral preferences with respect to the diurnal or seasonal timing of travel. As a smolt passed a receiver station, typically a few tag transmissions were recorded. The cluster of detections is termed a crossing event of a given fish at a given station (Melnychuk and Walters 2010). There were more than 6000 crossing events at stations in the lower Fraser River, lower reaches and upstream reaches of smaller rivers, and coastal straits at NSOG, QCS and JDF. Most crossing events in rivers occurred during May and June each year, usually within a few days after tagging and release. Duration of downstream travel was on average 4.5 ± 2.4 days (SD) for hatchery-reared release groups and 7.5 ± 4.5 days for wild groups in the Fraser River, and was on average 3.6 ± 3.7 days for hatchery-reared groups and 1.9 ± 2.5 days for wild groups in smaller rivers; coefficients of variation within release groups were similar on average to coefficients of variation among release groups. Most riverine migratory routes were unidirectional, but occasionally smolts were detected moving upstream or were detected in multiple crossing events at an in-river station. The time of day of the first detection of each crossing event was compared within and among habitat types (lower Fraser river; upper reaches of smaller rivers; lower reaches of smaller rivers; coastal straits) to assess possible diurnal patterns of travel.

### Table 1

**Sample sizes of salmon smolts tagged under the Pacific Ocean Shelf Tracking Project and included in the analysis**

<table>
<thead>
<tr>
<th>Watershed</th>
<th>Species</th>
<th>H/W*</th>
<th>2004</th>
<th>2005</th>
<th>Year</th>
<th>2006</th>
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<th>2008</th>
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<tr>
<td>Spius Creek</td>
<td>Chinook</td>
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<tr>
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<td>Sockeye</td>
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<tr>
<td>Fraser River, pooled release group labelled as “other”</td>
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<td>Chinook</td>
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<tr>
<td>Spius Creek</td>
<td>Coho</td>
<td>H</td>
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<td>49</td>
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<tr>
<td>Tenderfoot Creek</td>
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<tr>
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<td>Coho</td>
<td>H</td>
<td>60</td>
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<tr>
<td>Seymour River</td>
<td>Steelhead</td>
<td>H</td>
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<tr>
<td>Cowichan River</td>
<td>Steelhead</td>
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<tr>
<td>Englishman River</td>
<td>Steelhead</td>
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<td>67</td>
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<tr>
<td>Keogh River</td>
<td>Coho</td>
<td>W</td>
<td>107</td>
<td>49</td>
<td>50</td>
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<tr>
<td>Keogh River</td>
<td>Steelhead</td>
<td>H</td>
<td>92</td>
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<tr>
<td>Keogh River</td>
<td>Steelhead</td>
<td>W</td>
<td>78</td>
<td>50</td>
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<tr>
<td>Nimpkish River</td>
<td>Chinook</td>
<td>UN</td>
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<tr>
<td>Nimpkish River</td>
<td>Coho</td>
<td>H</td>
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<td>57</td>
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<tr>
<td>Nimpkish River</td>
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<td>W</td>
<td>50</td>
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</table>

Additional information about these release groups (body lengths; release dates; tag types) is given in Supplementary Material 1.

*Rearing history abbreviations: H, hatchery-reared; W, wild-caught without an adipose fin clipped so presumed wild; UN, unknown provenance since wild-caught but with unclipped hatchery fish released upstream.*
The light intensity associated with the first detection of each crossing event in lower river reaches was quantified. Solar illuminance is a measure of sunlight intensity, and depends on latitude, time of year, and time of day. Details of the calculation are described in Supplementary Material 2, and illuminance as a function of time of day is shown in Figure 2 for southern BC during the migration season. Illuminance was plotted against the Julian day of crossing events in lower river reaches to address whether smolts migrating later in the season were less selective in terms of diurnal travel timing preferences, and whether such patterns differed between the Fraser River (an eighth-order waterbody with mean annual discharge of 3600 m$^3$/s) and smaller rivers (waterbody orders ranging from 3 to 6, with mean annual discharges ranging from 4 to 238 m$^3$/s).

After documenting patterns of diurnal and seasonal timing of smolts, the possibility of whether variation in timing strategies affected survival from lower river reaches to coastal marine waters was addressed. After detection in lower river reaches, smolts migrating downstream may still be vulnerable to visual predation risk throughout the remainder of the lower river and estuary. Of the 3812 tagged smolts across 44 release groups, 679 were detected in the lower Fraser River and 1271 were detected in lower reaches of smaller rivers; this subset of 1950 fish comprised our dataset for the survival analysis. (Fish not detected in lower river reaches but later detected at ocean receivers were excluded because their riverine timing patterns are unknown.) The survival analysis thus conditions on fish detected in lower river reaches, which precludes the use of mark-recapture models. Instead, mixed-effects logistic regression was used, where the binary response variable represented subsequent detection or not at any of the NSOG, QCS, or JDF coastal stations (Figure 1). The response is therefore a joint probability of survival to coastal stations and detection at coastal stations. Because detection probability estimates at coastal stations were typically consistent from year to year for a given tag type (Melnychuk 2009a; Welch et al. 2011), averaging 89% for V9 tags and 65% for V7 tags, this joint probability is hereafter simply referred to as survival ($s$). To ensure that survival inferences are not sensitive to differences in detection probability of V7 and V9 tag models (which differ in acoustic output), the factor “TagType” was explicitly accounted for in survival models. Body length (“FL”) was also accounted for, as this has been commonly observed to affect fish survival in previous studies (Lorenzen 1996; Sogard 1997; Melnychuk 2009a). A random effect of release group was considered, where release groups $i$ consist of smolts $j$ of the same species, wild or hatchery-rearing history, watershed of origin, and year of release. Because 5 Fraser River release groups had <10 fish detected in lower river reaches, these were pooled into an “other” group (Bolker et al. 2009), for a total of 41 release groups. Each release group had an estimated random offset ($\omega_{ij}$) from the overall survival intercept; offsets were assumed to be normally distributed around zero with variance specified by an estimated hyperparameter, i.e., $\omega_{ij} \sim N(0, \sigma^2_{\omega0})$ (Pinheiro and Bates 2000). The base model, comprising no migration timing variables but only control factors, was thus:

$$\logit(s) = \alpha_i + \beta_{TagType} \cdot TagType_j + \beta_{FL} \cdot FL_j + \epsilon_{ij} \quad (1),$$

where $\alpha_i$ is an overall fixed intercept for survival, $\beta$ terms are coefficients for TagType and FL effects, and residual error $\epsilon_{ij}$ is normally-distributed after logit-transformation of $s$, i.e., $\epsilon_{ij} \sim N(0, \sigma^2_{\epsilon0})$. In abbreviated notation, the same model is specified as:

$$s \sim 1 + TagType + FL \mid \text{rand}(\omega_{ij}) \quad (2),$$

shown as model 1 in Table 2.

Building on the base model, candidate models were considered which involved: river size (“Rsize”), i.e., whether a fish was released and later detected in the Fraser River or in smaller rivers; the Julian day of the first crossing event in the lower river (“Date”); and the average illuminance associated with all crossing events in the lower river (“Light”). Other models further included an interaction between river size and Julian day, and/or between river size and illuminance (Table 2) to allow for possibilities that effects of migration timing on estuarine survival differ between the Fraser River and small rivers. A ninth model also allowed for a possible interaction of river size and body length on survival (Table 2), as size-related mortality effects may depend on river flow.

Two sensitivity analyses were conducted. The first treated species (4 categories), rearing history (3 categories), and year (5 categories) as fixed effects instead of being part of the release group random effect (Supplementary Material 3). The second considered the maximum illuminance rather than average illuminance for each fish, to allow for the possibility that visual predation risk depends more on maximum exposure than average exposure (Supplementary Material 4). The “glmer” function in the “lme4” (Bates et al. 2015) package for R (R Core Team 2017) was used with restricted maximum likelihood to compare candidate models, estimate fixed effect coefficients, and estimate conditional modes of random effects (Bolker et al. 2009). All numerical covariates were centered and standardized by their standard deviations prior to analyses. Generalized variance inflation factors were calculated to check for collinearity among predictor variables (Zuur et al. 2010).
before and after sunrise and sunset. The May 1 and June 1 reference lines bracket the release dates of most populations, but the observed nocturnal pattern was robust to migration times in April or June as well. Salmon smolts, whether originating from the Fraser River or from smaller rivers, showed no diurnal timing preference as they passed coastal receiver stations at NSOG, QCS, or JDF (Figure 3d). Frequency distributions were also examined separately by species and by wild or hatchery-rearing history (not shown), but no differences in diel migration timing were observed among these categories.

Contrary to expectation, salmon migrating later in the season were not less selective with respect to light intensity at the time of active travel downstream. If anything, there was a slight tendency for salmon smolts to pass receiver stations during low light periods later in the season than earlier in the season, in both the Fraser River (Figure 4a) and smaller rivers (Figure 4b). The tendency for juvenile salmon in the lower Fraser River to travel during times of brighter light than salmon in lower reaches of smaller rivers held across the entire migration season (Figure 4).

Among candidate models for predicting survival from lower river reaches to coastal stations, strong support was found for model 8 (Table 3). This model allowed for separate effects of light intensity on survival between the Fraser River and smaller rivers, as well as separate effects of the date of migration on survival. Model 9, which further included an interaction between river size and body length, had fairly strong support in terms of its AICc value (typically models with AICc < 2 from the best model are considered to also have strong support), but the additional interaction term only led to a further decrease of 0.8 in the deviance (Table 3), suggesting limited additional explanatory power. Models 6 and 7, which contained only one of the interaction terms, Rsizelight or RsizelDate, had low levels of support. Other models that included one or all 3 main effects but no interactions had essentially no support (Table 3).

Several factors included as predictor variables in model 8, the AICc-preferred model, showed strong effects on survival from lower river reaches to coastal straits (Table 4). Body length had a strong positive effect on survival ($\beta_{FL} = 0.462 \pm 0.102$ SE) of smolts from both the Fraser River (Figure 5a) and smaller rivers (Figure 5b). Mean predicted survival ranged from 19% (95% CI, 14–25%) in the Fraser River and 31% (95% CI, 26–37%) in other rivers at the smallest body sizes tagged to 74% (95% CI, 69–78%) in the Fraser River and 87% (95% CI, 84–90%) in other rivers at the largest body sizes tagged. The larger, louder V9 tags were associated with a slightly greater joint probability of estuarine survival and detection at coastal straits (Table 4). At mean values of numerical covariates, the average Fraser River release group had joint probabilities of survival and detection of 28% and 33% when tagged with V7 and V9 tags, respectively (or for non-Fraser groups, 44% and 50%, respectively), but the differences were not statistically significant. Applying average detection probabilities at coastal stations of 65% for V7 tags and 89% for V9 tags (Melnichuk 2009a; Welch et al. 2011) to approximately separate this joint probability, predicted survival probability from lower river reaches to coastal detection stations was 43% and 38% for Fraser River groups tagged with V7 and V9 tags, respectively, and for non-Fraser groups was 67% and 56%, respectively.

Strong habitat-mediated effects of migration timing strategies on early ocean survival were observed, represented by interactions of river size with light or river size with Julian day of detection in lower river reaches (Table 4). The avoidance of daylight travel by salmon smolts in small rivers (Figure 3b,c) resulted in greater survival to coastal marine detection arrays (mean 55% survival and detection; 95% CI, 50–61%) compared to the few smolts that did migrate through lower river reaches during high light periods (mean 24%; 95% CI, 17–31%; $\beta_{tag/size/Fraser:Light} = -0.463 \pm 0.086$ SE; Figure 5d). In contrast, there was no effect of light intensity during detection in the lower Fraser River on survival to coastal marine detection arrays ($\beta_{tag/size/Fraser:Light} = -0.037 \pm 0.096$ SE; Figure 5e). The effect on survival of Julian day of travel through lower river reaches differed between rivers. The latest migration dates through the lower Fraser River were associated with higher survival (mean 69%; 95% CI, 60–77%) than the earliest dates (mean 38%; 95% CI, 33–44%; Figure 5c), while in smaller rivers, the latest dates were associated with lower survival (mean 19%; 95% CI, 14–25%) than the earliest dates (mean 70%; 95% CI, 65–74%; Figure 5f). In the Fraser River, this effect occurred across release groups ($\beta_{tag/size/ Fraser:Date} = 0.665 \pm 0.170$ SE), but in smaller rivers, this pattern only occurred among, not within release groups as evidenced by the nonsignificant slope for migration date in smaller rivers ($\beta_{tag/size/ non-Fraser:Date} = -0.161 \pm 0.178$ SE; Table 4).

Conditional modes of release groups ranged from $-1.45$ to 1.39 for Fraser River release groups, and ranged from $-1.97$ to 1.99 for release groups from smaller rivers (Figure 6). These represent random offsets from the overall fixed intercept for survival, evaluated at the best-fit values of fixed parameters and at mean values of
numerical predictor variables. Adding the conditional mode for a particular release group to the overall fixed intercept value (−0.934 in logit space, Table 4) results in a survival intercept (in logit space) for that release group. Estimates of the variance hyperparameter, $\sigma^2_\omega$, ranged from 1.24 to 1.63 across models, with an estimate of $\sigma^2_\omega = 1.27$ for the AICc-preferred model 8.

All 9 candidate models (as well as all models in Supplementary Materials 3 and 4) converged. Generalized variance inflation factors were <2 for all fixed effect terms in model 8, suggesting limited concern for collinearity among predictor variables (Zuur et al. 2010). The sensitivity analysis in which species, rearing history, and year were treated as fixed effects instead of as part of random effect release groups led to similar conclusions about the effects of body length, light intensity, and migration date on survival, detailed in Supplementary Material 3. On the basis of AICc scores, the main run models (with species, rearing history, and year as part of random effects) outperformed sensitivity run models. The second sensitivity analysis that considered the maximum illuminance rather than average illuminance for each fish led to similar results and qualitative conclusions, detailed in Supplementary Material 4.

DISCUSSION

Support was found for hypothesis (1) that migrating through lower river reaches during daylight hours had greater deleterious survival consequences in the estuaries of small rivers than in the estuary of the larger Fraser River. This survival difference between rivers is plausibly attributed to differences in visual predation risk. Compared to smaller rivers, the mainstem Fraser River has extreme silt loads which reduce light levels to near zero within centimeters of the surface, and also offers a higher water column away from bottom-oriented predators, which may both reduce the risk of visual predation during daylight hours (Gregory and Levings 1998;
Mackas). Nocturnal travel provides a
change in river size per se.
Table 3.
Comparison of mixed-effects logistic regression models for the joint probability of survival from lower river reaches to coastal detection stations and detection at those coastal stations

<table>
<thead>
<tr>
<th>Model</th>
<th>–2 ln(L)</th>
<th>df</th>
<th>AICc</th>
<th>ΔAICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>8. ... + Rszie + Date + Light + Rszie:Date + Rszie:Light</td>
<td>2246.8</td>
<td>9</td>
<td>2265.6</td>
<td>0.0</td>
</tr>
<tr>
<td>9. ... + Rszie + Date + Light + Rszie:Date + Rszie:Light + Rszie:FL.</td>
<td>2262.8</td>
<td>8</td>
<td>2278.8</td>
<td>13.2</td>
</tr>
<tr>
<td>6. ... + Rszie + Date + Light + Rszie:Light</td>
<td>2272.9</td>
<td>8</td>
<td>2286.9</td>
<td>21.3</td>
</tr>
<tr>
<td>7. ... + Rszie + Date + Light + Rszie:Date</td>
<td>2292.4</td>
<td>5</td>
<td>2302.4</td>
<td>24.4</td>
</tr>
<tr>
<td>5. ... + Rszie + Date + Light</td>
<td>2293.2</td>
<td>5</td>
<td>2301.6</td>
<td>36.8</td>
</tr>
<tr>
<td>4. ... + Light</td>
<td>2293.1</td>
<td>5</td>
<td>2301.1</td>
<td>39.5</td>
</tr>
<tr>
<td>3. ... + Date</td>
<td>2292.0</td>
<td>5</td>
<td>2298.9</td>
<td>41.3</td>
</tr>
<tr>
<td>2. ... + Rszie</td>
<td>2292.1</td>
<td>5</td>
<td>2302.4</td>
<td>41.3</td>
</tr>
<tr>
<td>1. base model*</td>
<td>2292.0</td>
<td>5</td>
<td>2302.4</td>
<td>41.3</td>
</tr>
</tbody>
</table>

Criteria include the deviance (twice the negative log-likelihood, –2·ln(L)), degrees of freedom (df), Akaike Information Criterion adjusted for sample size (AICc), and difference in AICc from the AICc-best model.

*base model is: s ~ 1 + TagType + FL | rand(σ₀), where s is a joint probability of survival and detection.

Table 4.
Estimated coefficients of fixed effects for model 8, the AICc-preferred model

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>CL</th>
<th>95%</th>
<th>CL</th>
<th>95%</th>
<th>c²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Overall intercept</td>
<td>-0.934</td>
<td>-1.685</td>
<td>-0.182</td>
<td>-2.43</td>
<td></td>
<td></td>
</tr>
<tr>
<td>TagType/V9b</td>
<td>0.243</td>
<td>-0.368</td>
<td>0.853</td>
<td>0.78</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rszie</td>
<td>0.462</td>
<td>0.261</td>
<td>0.662</td>
<td>4.25</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rszie:Fraser:Light</td>
<td>0.684</td>
<td>-0.114</td>
<td>1.482</td>
<td>1.68</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rszie:Fraser:Date</td>
<td>0.037</td>
<td>-0.150</td>
<td>0.225</td>
<td>0.39</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rszie:non-Fraser:Light</td>
<td>-0.463</td>
<td>-0.632</td>
<td>-0.295</td>
<td>-3.39</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rszie:non-Fraser:Date</td>
<td>-0.665</td>
<td>0.332</td>
<td>0.998</td>
<td>3.91</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rszie/non-Fraser:Date</td>
<td>-0.161</td>
<td>-0.511</td>
<td>0.189</td>
<td>-0.90</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Numerical covariates were centered and standardized by their standard deviations. To ease comparisons, the model is specified with slopes for “Date” and “Light” that are specific to Fraser and non-Fraser rivers rather than specified with main effects and interaction discrepancies as shown in Table 3, but these 2 models are statistically identical.

*|c²| > 2 generally suggests statistical significance at α = 0.05.
Reference groups: “V7”. “Fraser”.

Although the coastal detection stations were typically tens to hundreds of kilometres away from river mouths, any survival differences among individuals established in the remainder of the riverine and estuarine migration would reasonably persist to coastal stations given that the distance from lower rivers to coastal stations is the same among individuals. The inclusion of only one large river in our study precludes generalization about differences between large and small rivers; observed differences in survival and diel migration behavior between the Fraser River and smaller rivers may result more from differences in water clarity than from differences in river size per se.

Support was also found for hypothesis (2) that juvenile salmon change their diel migration patterns in small, clear-water rivers in which they are particularly vulnerable, presumably to reduce their exposure to visual predators. Strong preferences for nocturnal travel in small, clear rivers have also been observed previously (Hoar 1951; McDonald 1960; Greenstreet et al. 1993; Wood et al. 1993; Moore et al. 1995; Melnychuk et al. 2007; Chapman et al. 2013), including 2 studies in which migration was predominantly nocturnal in clearer rivers but more evenly distributed in turbid rivers (Chase et al. 2013; Clark et al. 2016). Nocturnal travel provides a temporal offset from when salmon predators forage more efficiently, i.e., during daylight hours (Mann 1982; Mace 1983; Greenstreet et al. 1993; Railsback et al. 2005). This behavior is presumably adaptive, as there was a strong effect of diel migration timing on survival to coastal marine waters (hypothesis 1), and the timing of migration is heritable (Taylor 1990). Conversely, there was no observed effect of diel migration timing in the lower Fraser River on survival to coastal straits, nor was there any observed preference for nocturnal travel. The observed difference among rivers in diurnal migration behavior therefore likely reflects different selection pressures, similar to how diel foraging patterns of salmonids differ between habitats that vary in predation risk (Railsback et al. 2005). Consistent with hypothesis (1), the strategy of avoiding daylight travel in small, clear rivers appears to carry an estuarine survival advantage, whereas no survival advantage seems to be present in the larger Fraser River which confers a lower visual predation risk.

Avoiding downstream travel during daylight hours delays ocean entry. Distances from release point to lower river reaches were greater for all Fraser River groups (most groups >300 km) than for release groups from smaller rivers (all <65 km), but downstream travel times were similar, averaging 5.1 days for Fraser River groups and 3.6 days for groups from smaller rivers. The faster average travel speeds down the Fraser River compared to smaller rivers (Melnychuk et al. 2010) may result partly from faster water velocity, but also from smolts migrating during daytime hours. By restricting travel to nighttime hours in smaller rivers, smolts spent a greater proportion of their time not actively migrating. For example, in mid-May at the latitude of these rivers, the time from sunset to sunrise is approximately 8 h, so smolts would achieve average migration speeds of only one-third the speed of continuously-migrating smolts. After ocean entry from small rivers, average travel speeds increased (Melnychuk et al. 2010) as smolts began migrating during daylight hours as well.

No support was found for hypothesis (3) that juvenile salmon migrating later in the season are less selective with respect to diel timing preferences. Average light intensity during which smolts were detected in lower river reaches did not increase over the migration season in either the Fraser River or smaller rivers, as has been previously found and attributed either to increasing temperature (Fraser et al. 1993; Ibbotson et al. 2006) or to optimal time of ocean arrival (Moore et al. 1995). Ocean entry prior to May would precede periods of high zooplankton abundance (Mackas...
et al. 2013; Peña et al. 2016), but delaying ocean entry too long offers less time for juvenile salmon to grow and build up lipid stores which are thought to be important for surviving the first marine winter (Beamish and Mahnken 2001). Ocean entry dates of these salmon populations are typically within periods of high zooplankton availability in the Strait of Georgia throughout May and June (Mackas et al. 2013; Peña et al. 2016). During this smolt migration season, daylight hours lengthen and average cloud cover typically lessens. Although it might delay ocean entry by a few days, there may be even greater incentive to favor nocturnal travel as the season progresses because visual exposure and therefore risk of predation likely increase.

The influence of ocean entry timing on survival to coastal waters differed between the Fraser River and smaller rivers. There was a post-hoc negative correlation between conditional modes (i.e., random offsets from the overall fixed intercept for survival) and average migration date of release groups in both the Fraser River ($r = -0.55$) and smaller rivers ($r = -0.30$), but in the Fraser River this was countered by an even stronger positive relationship within release groups (Table 4), which may be related to river flow. The Fraser River’s plume extends far into the Strait of Georgia, and average daily flow increases throughout the migration season (Melnychuk 2009b), so later-migrating individuals may be assisted by currents to a greater extent even after ocean entry, thereby reducing predation risk. The positive relationship between survival and migration date is opposite to the general pattern found for smolt-to-adult survival of steelhead and Chinook salmon in another large river, the Columbia River (Scheuerell et al. 2009), but daily flow generally follows the opposite pattern in the Columbia River, decreasing over the migration season. Results are thus consistent between studies, with higher survival probability associated with greater water flow experienced by individual smolts, with at least part of this improved survival attributable to smolts passing a fixed detection point more quickly when water flows are more rapid.

Behavioral timing decisions of individuals during migration periods may depend not only on time of day or time of year per se, but depend also on the timing decisions made by conspecifics. Predation risk for any given individual may be diluted by density-dependent predator swamping mechanisms as comigrants travel together (Furey et al. 2016). With respect to diel migration patterns, the survival advantage conferred by nocturnal migration in small clear rivers may in part be attributable to a greater density of exposed smolts during nighttime hours than during daylight hours (as smolts appear to hide during daylight hours, reducing their exposure to visual predation). With respect to seasonal migration patterns, the trade-off faced by any individual of early travel downstream (for the growth advantages predicted from earlier ocean entry) and delayed travel downstream (for the reduction in visual predation risk by restricting in-river travel to nighttime hours) may equally be influenced by the timing decisions made by other migrating smolts.

**CONCLUSIONS**

The probability of survival is strongly influenced by behavioral decisions during times of high vulnerability to predation risk, such as periods of foraging, mating, and migrating (Lima and Dill 1990; Smith and McWilliams 2014; Hertel et al. 2017). The period of estuarine and early ocean migration is thought to be a bottleneck
for juvenile salmon survival (Healey 1980; Mace 1983; Greenstreet et al. 1993), and this study shows that different timing strategies have a strong influence on the chance of surviving this period. Further, we demonstrate across several watersheds that the behavioral timing decisions affecting estuarine survival are mediated by riverine characteristics, in particular water visibility. These observations have important implications for hatchery release strategies, as temperature increases from climate change are predicted to accelerate the timing of downstream migration and ocean entry (Achord et al. 2007; Beamish et al. 2008; Spence and Dick 2014), which this study suggests may increase survival of juvenile salmon from small coastal rivers but decrease survival of salmon from the larger Fraser River.

**SUPPLEMENTARY MATERIAL**

Supplementary data are available at *Behavioral Ecology* online.

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provided helpful comments. John Beeman and Russell Perry provided helpful thoughts during discussions.

Data accessibility: Analyses reported in this article can be reproduced using the data provided by Melnychuk and Welch (2018). All raw detection data forming the basis for this analysis are freely available from the Ocean Tracking Network data portal, https://members.oceantrack.org/projects. (Accessed 27 August 2018).

Handling editor: John Fitzpatrick

REFERENCES


Smith AD, McWilliams SR. 2014. What to do when stopping over: behavioral decisions of a migrating songbird during stopover are dictated by initial change in their body condition and mediated by key environmental conditions. Behav Ecol. 25:1423–1435.


## Supplementary material 1.

### Table S1-1. Body lengths, release dates, and tag types used for salmon smolt populations tagged under the Pacific Ocean Shelf Tracking Project (POST) from 2004–2008 and included in the analysis

<table>
<thead>
<tr>
<th>Watershed</th>
<th>Species a</th>
<th>H/W b</th>
<th>Year</th>
<th>n c</th>
<th>Mean FL ± SD (Range) d</th>
<th>Release date(s) (n) e</th>
<th>Tag type(s) (n) f</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fraser River</td>
<td>Chnk</td>
<td>H</td>
<td>2006</td>
<td>100</td>
<td>151.2 ± 17.1 (125–186)</td>
<td>Apr 18 13:15</td>
<td>V7-2L</td>
</tr>
<tr>
<td>Coldwater River</td>
<td>Chnk</td>
<td>UN</td>
<td>2005</td>
<td>69</td>
<td>139.3 ± 11.2 (121–177)</td>
<td>May 04 20:00 (58), May 08 20:00 (11)</td>
<td>V7-2L (50), V9-6L (19)</td>
</tr>
<tr>
<td>Coldwater River</td>
<td>Chnk</td>
<td>H</td>
<td>2006</td>
<td>100</td>
<td>130.1 ± 3.3 (125–141)</td>
<td>May 29 13:00</td>
<td>V7-2L</td>
</tr>
<tr>
<td>Coldwater River</td>
<td>Coho</td>
<td>H</td>
<td>2006</td>
<td>100</td>
<td>130.1 ± 3.3 (125–141)</td>
<td>May 29 13:00</td>
<td>V7-2L</td>
</tr>
<tr>
<td>Coldwater River</td>
<td>Sth</td>
<td>W</td>
<td>2004</td>
<td>31</td>
<td>154.4 ± 18.9 (125–204)</td>
<td>Apr 16 23:00 (2), May 07 20:00 (4), May 15 20:00 (16), May 31 21:15 (9)</td>
<td>V9-6L</td>
</tr>
<tr>
<td>Coldwater River</td>
<td>Sth</td>
<td>W</td>
<td>2005</td>
<td>50</td>
<td>170.6 ± 15.4 (142–219)</td>
<td>Apr 20 20:00 (1), May 04 20:00 (11), May 08 20:00 (4), May 19 20:00 (17), May 29 21:30 (17)</td>
<td>V9-6L,</td>
</tr>
<tr>
<td>Watershed</td>
<td>Species&lt;sup&gt;a&lt;/sup&gt;</td>
<td>H/W&lt;sup&gt;b&lt;/sup&gt;</td>
<td>Year</td>
<td>n&lt;sup&gt;c&lt;/sup&gt;</td>
<td>Mean FL ± SD (Range)&lt;sup&gt;d&lt;/sup&gt;</td>
<td>Release date(s) (n)&lt;sup&gt;e&lt;/sup&gt;</td>
<td>Tag type(s) (n)&lt;sup&gt;f&lt;/sup&gt;</td>
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<td>-----------------------------</td>
</tr>
<tr>
<td>Coldwater River</td>
<td>Sth</td>
<td>W</td>
<td>2006</td>
<td>75</td>
<td>162.3 ± 13.1 (140–198)</td>
<td>May 07 20:00 (56), May 18 20:00 (19)</td>
<td>V7-2L (25), V9-6L (50)</td>
</tr>
<tr>
<td>Nicola River</td>
<td>Chnk</td>
<td>H</td>
<td>2005</td>
<td>50</td>
<td>117.1 ± 3.1 (112–127)</td>
<td>May 02 15:39</td>
<td>V7-2L</td>
</tr>
<tr>
<td>Spius Creek</td>
<td>Chnk</td>
<td>H</td>
<td>2006</td>
<td>99</td>
<td>128.6 ± 4.4 (123–142)</td>
<td>Apr 20 10:35</td>
<td>V7-2L</td>
</tr>
<tr>
<td>Deadman River</td>
<td>Sth</td>
<td>W</td>
<td>2005</td>
<td>57</td>
<td>166.5 ± 18.8 (142–227)</td>
<td>Apr 22 21:15 (9), Apr 27 21:30 (8), May 05 23:30 (11), May 17 21:45 (6), May 30 21:15 (23)</td>
<td>V9-6L</td>
</tr>
<tr>
<td>Deadman River</td>
<td>Sth</td>
<td>W</td>
<td>2006</td>
<td>64</td>
<td>163.2 ± 20.5 (128–209)</td>
<td>May 08 12:00 (3), May 19 22:00 (12), May 28 22:00 (10), Jun 10 22:00 (12), Jun 19 21:30 (22), Jul 01 21:30 (5)</td>
<td>V7-2L (26), V9-6L (38)</td>
</tr>
<tr>
<td>Cultus Lake</td>
<td>Sock</td>
<td>H</td>
<td>2004</td>
<td>100</td>
<td>177.6 ± 12.5 (142–210)</td>
<td>May 03 20:30</td>
<td>V9-6L</td>
</tr>
<tr>
<td>Cultus Lake</td>
<td>Sock</td>
<td>H</td>
<td>2005</td>
<td>376</td>
<td>176.8 ± 13.8 (148–216)</td>
<td>Jun 08 20:00</td>
<td>V9-1L (92), V9-2L (188), V9-6L (96),</td>
</tr>
<tr>
<td>Watershed</td>
<td>Species</td>
<td>H/W</td>
<td>Year</td>
<td>n</td>
<td>Mean FL ± SD (Range)</td>
<td>Release date(s) (n)</td>
<td>Tag type(s) (n)</td>
</tr>
<tr>
<td>-------------------</td>
<td>---------</td>
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<td>------</td>
<td>----</td>
<td>----------------------</td>
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<td>-----------------</td>
</tr>
<tr>
<td>Cultus Lake</td>
<td>Sock</td>
<td>H</td>
<td>2006</td>
<td>200</td>
<td>178.3 ± 8.9  (164–204)</td>
<td>Apr 20 18:00</td>
<td>V9-1L</td>
</tr>
<tr>
<td>Cultus Lake</td>
<td>Sock</td>
<td>H</td>
<td>2007</td>
<td>319</td>
<td>182.2 ± 7.3  (160–217)</td>
<td>Apr 26 15:00</td>
<td>V9-6L (119)</td>
</tr>
<tr>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td>May 16 15:00</td>
<td>V9-1L (200)</td>
</tr>
</tbody>
</table>

Fraser River, pooled release group labelled as “other”

<table>
<thead>
<tr>
<th>Watershed</th>
<th>Species</th>
<th>H/W</th>
<th>Year</th>
<th>n</th>
<th>Mean FL ± SD (Range)</th>
<th>Release date(s) (n)</th>
<th>Tag type(s) (n)</th>
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<tbody>
<tr>
<td>Coldwater River</td>
<td>Chnk</td>
<td>W</td>
<td>2004</td>
<td>4</td>
<td>136.8 ± 8.9  (128–143)</td>
<td>May 07 20:00 (2),</td>
<td>V9-6L</td>
</tr>
<tr>
<td></td>
<td></td>
<td>UN</td>
<td></td>
<td></td>
<td></td>
<td>May 15 20:00 (2)</td>
<td></td>
</tr>
<tr>
<td>Coldwater River</td>
<td>Coho</td>
<td>H</td>
<td>2004</td>
<td>40</td>
<td>130.8 ± 2.7  (127–141)</td>
<td>May 31 14:00</td>
<td>V7-2L (12),</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td>V9-6L (28)</td>
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<tr>
<td>Nicola River</td>
<td>Chnk</td>
<td>H</td>
<td>2004</td>
<td>49</td>
<td>129.4 ± 4.8  (120–142)</td>
<td>Apr 21 10:00</td>
<td>V9-6L</td>
</tr>
<tr>
<td>Spius Creek</td>
<td>Coho</td>
<td>H</td>
<td>2005</td>
<td>50</td>
<td>128.4 ± 3.9  (122–141)</td>
<td>May 19 11:15</td>
<td>V7-2L</td>
</tr>
</tbody>
</table>

Smaller rivers

<table>
<thead>
<tr>
<th>Watershed</th>
<th>Species</th>
<th>H/W</th>
<th>Year</th>
<th>n</th>
<th>Mean FL ± SD (Range)</th>
<th>Release date(s) (n)</th>
<th>Tag type(s) (n)</th>
</tr>
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<tbody>
<tr>
<td>Cheakamus River</td>
<td>Sth</td>
<td>H</td>
<td>2007</td>
<td>100</td>
<td>183.3 ± 11.2  (163–210)</td>
<td>May 06 16:00 (19)</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>May 23 12:30 (81)</td>
<td></td>
</tr>
<tr>
<td>Watershed</td>
<td>Species&lt;sup&gt;a&lt;/sup&gt;</td>
<td>H/W&lt;sup&gt;b&lt;/sup&gt;</td>
<td>Year</td>
<td>n&lt;sup&gt;c&lt;/sup&gt;</td>
<td>Mean FL ± SD (Range)&lt;sup&gt;d&lt;/sup&gt;</td>
<td>Release date(s) (n)&lt;sup&gt;e&lt;/sup&gt;</td>
<td>Tag type(s) (n)&lt;sup&gt;f&lt;/sup&gt;</td>
</tr>
<tr>
<td>-------------------</td>
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<td>-------------------------------</td>
<td>---------------------------------</td>
<td>-----------------------------</td>
</tr>
<tr>
<td>Cheakamus River</td>
<td>Sth</td>
<td>H</td>
<td>2008</td>
<td>98</td>
<td>181.7 ± 11.1 (155–206)</td>
<td>May 08 11:17 (40), May 22 09:37 (18), May 05 16:00 (40)</td>
<td>V9-6L</td>
</tr>
<tr>
<td>Cheakamus River</td>
<td>Sth</td>
<td>W</td>
<td>2004</td>
<td>51</td>
<td>184.5 ± 17.3 (148–226)</td>
<td>May 08 20:45 (42), May 24 18:00 (9)</td>
<td>V9-6L</td>
</tr>
<tr>
<td>Cheakamus River</td>
<td>Sth</td>
<td>W</td>
<td>2005</td>
<td>49</td>
<td>177.6 ± 14 (153–212)</td>
<td>May 06 20:25 (44), May 19 20:20 (5)</td>
<td>V9-6L</td>
</tr>
<tr>
<td>Cheakamus River</td>
<td>Sth</td>
<td>W</td>
<td>2008</td>
<td>100</td>
<td>177.9 ± 11.9 (149–209)</td>
<td>May 06 19:30 (72), May 12 20:30 (28)</td>
<td>V9-6L</td>
</tr>
<tr>
<td>Tenderfoot Creek</td>
<td>Coho</td>
<td>H</td>
<td>2004</td>
<td>100</td>
<td>140.2 ± 6.6 (130–159)</td>
<td>May 10 18:00</td>
<td>V9-6L</td>
</tr>
<tr>
<td>Tenderfoot Creek</td>
<td>Coho</td>
<td>H</td>
<td>2005</td>
<td>100</td>
<td>138.1 ± 7.3 (123–155)</td>
<td>May 11 15:00</td>
<td>V7-2L (50), V9-6L (50)</td>
</tr>
<tr>
<td>Tenderfoot Creek</td>
<td>Coho</td>
<td>H</td>
<td>2006</td>
<td>120</td>
<td>138.9 ± 9.9 (125–165)</td>
<td>May 04 16:00</td>
<td>V7-2L (70), V9-6L (50)</td>
</tr>
<tr>
<td>Tenderfoot Creek</td>
<td>Coho</td>
<td>H</td>
<td>2007</td>
<td>199</td>
<td>132.2 ± 5.5 (125–147)</td>
<td>May 10 16:00</td>
<td>V7-2L</td>
</tr>
<tr>
<td>Watershed</td>
<td>Species&lt;sup&gt;a&lt;/sup&gt;</td>
<td>H/W&lt;sup&gt;b&lt;/sup&gt;</td>
<td>Year</td>
<td>n&lt;sup&gt;c&lt;/sup&gt;</td>
<td>Mean FL ± SD (Range)&lt;sup&gt;d&lt;/sup&gt;</td>
<td>Release date(s) (n)&lt;sup&gt;e&lt;/sup&gt;</td>
<td>Tag type(s) (n)&lt;sup&gt;f&lt;/sup&gt;</td>
</tr>
<tr>
<td>-----------------</td>
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<td>------</td>
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<td>--------------------------------</td>
<td>---------------------------------</td>
<td>-----------------------------</td>
</tr>
<tr>
<td>Seymour River</td>
<td>Coho</td>
<td>H</td>
<td>2007</td>
<td>60</td>
<td>128.7 ± 13.8 (124–139)</td>
<td>Apr 26 08:00 (35), May 05 08:00 (25)</td>
<td>V7-2L</td>
</tr>
<tr>
<td>Seymour River</td>
<td>Sth</td>
<td>H</td>
<td>2007</td>
<td>60</td>
<td>185.9 ± 12.6 (160–224)</td>
<td>Apr 27 15:15 (20), May 08 14:50 (20), May 15 12:00 (20)</td>
<td>V9-6L</td>
</tr>
<tr>
<td>Cowichan River</td>
<td>Sth</td>
<td>H</td>
<td>2006</td>
<td>50</td>
<td>177.8 ± 13.8 (156–200)</td>
<td>May 09 15:10</td>
<td>V9-6L</td>
</tr>
<tr>
<td>Englishman River</td>
<td>Sth</td>
<td>W</td>
<td>2004</td>
<td>67</td>
<td>174.4 ± 16.9 (132–210)</td>
<td>May 13 22:00 (12), May 14 22:30 (7), May 15 22:30 (12), May 17 21:40 (12), May 18 21:40 (9), May 19 21:30 (4), May 20 21:30 (6), May 21 22:00 (1), May 22 22:10 (2), May 23 22:00 (2)</td>
<td>V9-6L</td>
</tr>
<tr>
<td>Englishman River</td>
<td>Sth</td>
<td>W</td>
<td>2005</td>
<td>43</td>
<td>159.4 ± 14.8 (133–196)</td>
<td>May 13 21:00 (11), May 18 21:30 (12), May 19 19:00 (14), May 23 11:30 (6)</td>
<td>V9-6L</td>
</tr>
<tr>
<td>Watershed</td>
<td>Species a</td>
<td>H/W b</td>
<td>Year</td>
<td>n c</td>
<td>Mean FL ± SD (Range) d</td>
<td>Release date(s) (n) e</td>
<td>Tag type(s) (n) f</td>
</tr>
<tr>
<td>-----------------</td>
<td>-----------</td>
<td>-------</td>
<td>------</td>
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<td>------------------------</td>
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<td>-------------------</td>
</tr>
<tr>
<td>Englishman River</td>
<td>Sth</td>
<td>W</td>
<td>2006</td>
<td>50</td>
<td>168.7 ± 12.5 (149–206)</td>
<td>May 03 17:00 (8), May 04 21:00 (6), May 05 21:00 (16), May 07 21:00 (20)</td>
<td>V9-6L</td>
</tr>
<tr>
<td>Keog River</td>
<td>Coho</td>
<td>W</td>
<td>2004</td>
<td>107</td>
<td>154.6 ± 6.8 (139–173)</td>
<td>May 27 09:30 (37), May 27 22:00 (40), May 28 22:00 (30)</td>
<td>V9-6L</td>
</tr>
<tr>
<td>Keog River</td>
<td>Coho</td>
<td>W</td>
<td>2005</td>
<td>49</td>
<td>157.5 ± 10.5 (143–183)</td>
<td>May 01 19:30</td>
<td>V9-6L</td>
</tr>
<tr>
<td>Keog River</td>
<td>Coho</td>
<td>W</td>
<td>2006</td>
<td>50</td>
<td>152.4 ± 18.6 (140–240)</td>
<td>May 07 19:30 (20), May 10 21:00 (30)</td>
<td>V9-6L</td>
</tr>
<tr>
<td>Keog River</td>
<td>Sth</td>
<td>H</td>
<td>2004</td>
<td>92</td>
<td>188 ± 18.4 (150–231)</td>
<td>May 17 16:00 (50), May 19 11:00 (42)</td>
<td>V9-6L</td>
</tr>
<tr>
<td>Keog River</td>
<td>Sth</td>
<td>H</td>
<td>2005</td>
<td>50</td>
<td>204 ± 14.7 (163–247)</td>
<td>May 25 16:00</td>
<td>V9-6L</td>
</tr>
<tr>
<td>Keog River</td>
<td>Sth</td>
<td>W</td>
<td>2004</td>
<td>78</td>
<td>174.6 ± 20 (147–250)</td>
<td>May 27 09:30 (25), May 27 22:00 (8), May 28 22:00 (13), May 29 22:00 (9), Jun 04 22:00 (23)</td>
<td>V9-6L</td>
</tr>
<tr>
<td>Watershed</td>
<td>Species&lt;sup&gt;a&lt;/sup&gt;</td>
<td>H/W&lt;sup&gt;b&lt;/sup&gt;</td>
<td>Year</td>
<td>n&lt;sup&gt;c&lt;/sup&gt;</td>
<td>Mean FL ± SD (Range)&lt;sup&gt;d&lt;/sup&gt;</td>
<td>Release date(s) (n)&lt;sup&gt;e&lt;/sup&gt;</td>
<td>Tag type(s) (n)&lt;sup&gt;f&lt;/sup&gt;</td>
</tr>
<tr>
<td>----------------</td>
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</tr>
<tr>
<td>Keogh River</td>
<td>Sth</td>
<td>W</td>
<td>2006</td>
<td>50</td>
<td>184 ± 17.1 (159–232)</td>
<td>May 31 19:30</td>
<td>V9-6L</td>
</tr>
<tr>
<td>Nimpkish River</td>
<td>Chnk</td>
<td>UN</td>
<td>2006</td>
<td>50</td>
<td>139 ± 9.6 (126–171)</td>
<td>May 08 19:00</td>
<td>V7-2L</td>
</tr>
<tr>
<td>Nimpkish River</td>
<td>Coho</td>
<td>H</td>
<td>2004</td>
<td>99</td>
<td>140.6 ± 4.2 (125–151)</td>
<td>Apr 28 18:00 (2), Jun 14 15:30 (97)</td>
<td>V9-6L</td>
</tr>
<tr>
<td>Nimpkish River</td>
<td>Coho</td>
<td>H</td>
<td>2005</td>
<td>57</td>
<td>130.9 ± 7 (122–149)</td>
<td>Jun 17 16:00</td>
<td>V7-2L (49), V9-6L (8)</td>
</tr>
<tr>
<td>Nimpkish River</td>
<td>Coho</td>
<td>W</td>
<td>2006</td>
<td>50</td>
<td>145.9 ± 4.8 (140–165)</td>
<td>May 11 16:20</td>
<td>V9-6L</td>
</tr>
</tbody>
</table>

<sup>a</sup> Species abbreviations: Chnk, Chinook; Sock, sockeye; Sth, steelhead.

<sup>b</sup> Rearing history abbreviations: H, hatchery-reared; W, wild-caught without an adipose fin clipped so presumed wild; UN, unknown provenance since wild-caught but with unclipped hatchery fish released upstream.

<sup>c</sup> n = number of smolts tagged and released. For groups with >1 release date or >1 tag type used, sample sizes are given in parentheses for each release date or each tag type.

<sup>d</sup> FL = fork length, in mm.

<sup>e</sup> Release times are Pacific daylight savings times.
†Lengths, weights, and total sample sizes of VEMCO tags used were: V7-2L (20 mm x 7 mm diameter, 1.6 g in air, \( n = 990 \)); V9-6L (21 x 9 mm diameter, 2.9 g in air, \( n = 2142 \)); V9-1L (24 x 9 mm, 3.6 g, \( n = 492 \)); and V9-2L (29 x 9 mm, 4.7 g, \( n = 188 \)).
Supplementary material 2. Calculation of illuminance

Solar illuminance is a measure of sunlight intensity received at the Earth’s surface at a given time and place, typically measured in units of lux (lx), or lumens per square metre, lm·m⁻². It depends on latitude, solar declination angle (which depends on time of year), and hour angle (time of day). Illuminance ($E_v$) is calculated as a function of time of day for a given location and date:

\[
E_v = \max\left(0, \ S \cdot \cos(Z)\right),
\]

where $Z$ is the zenith angle and $S$ is the illuminance on a clear day on a surface perpendicular to incoming solar radiation, at solar noon. A value of 129,032 was assumed for $S$, which scales $E_v$ to have a maximum of 110 kilolux (klx). $Z$ was calculated as:

\[
Z = \cos^{-1}\left(\sin \Phi \cdot \sin \delta + \cos \Phi \cdot \cos \delta \cdot \cos H\right),
\]

where $\Phi$ is latitude, $\delta$ is the solar declination angle, and $H$ is the hour angle. Values of $\Phi = 50^\circ$ and $\delta = 18.49^\circ$ were assumed, where $\delta$ is specified for May 15, the approximate middle of the migration season. $H$ was calculated as:

\[
H = 15^\circ \cdot (\text{hour} - 14.167),
\]

where $\text{hour}$ represents the number of hours since midnight and 14.167 is the time of solar noon in the study area (i.e., 2:10 p.m.). Illuminance was calculated as a function of time of day (Figure 2). The time of day of the first detection of each salmon crossing event in lower river reaches was paired with the corresponding value of $E_v$ to represent light intensity at the time of detection.
Supplementary material 3. Sensitivity analysis with species, rearing history, and year treated as fixed effects

The mixed-effects logistic regression in the main text involved random effect intercept offsets, $\omega_{0i}$, for separate release groups (Eq. 1). There were 41 such release groups (including an “other” group), comprised of unique combinations of species, rearing history, year, and watershed. In this sensitivity analysis, species (4 categories), rearing history (3 categories), and year (5 categories) are instead treated as fixed effects, while watershed remains a random effect intercept offset ($\omega_{0*}$) from the overall fixed-effect survival intercept. Random offsets for watershed are assumed normally distributed around zero with variance specified by an estimated hyperparameter, i.e., $\omega_{0*} \sim N(0, \sigma_{\omega_{0*}}^2)$. The base model for this sensitivity analysis thus becomes:

(S3-1) \[ \logit(s_{ij}) = \alpha_{0*} + \beta_{Spp} \cdot Spp_j + \beta_{HW} \cdot HW_j + \beta_{Year} \cdot Year_j + \beta_{TagType} \cdot TagType_j + \ldots + \beta_{FL} \cdot FL_j + \epsilon_{0j} \]

\[ \alpha_{0*} = \alpha_{0*} + \omega_{0*} \]

where $\alpha_{0*}$ is an overall fixed intercept for survival, $\beta$ terms are coefficients for species (“Spp”), rearing history (“HW”), year, TagType and FL effects, and residual error $\epsilon_{0j}$ is normally-distributed after logit-transformation of $s$, i.e., $\epsilon_{0j} \sim N(0, \sigma_{\epsilon_{0j}}^2)$. In abbreviated notation, the same model is specified as:

(S3-2) \[ s \sim 1 + Spp + HW + Year + TagType + FL | \text{rand}(\omega_{0*}) \]

shown as model S1 in Table S3-1. Other candidate models build on this base model, providing nine candidate models (Table S3-1) analogous to the nine candidate models in
the main analysis (Table 2). The response variable remains unchanged as the joint probability of survival from lower river reaches to coastal stations and detection at those coastal stations. This treatment of species, rearing history, and year allows for directly assessing overall differences in survival among the different categories of each of these variables.

All survival analyses were repeated under this alternative model formulation. In terms of AICc scores, the ranking of models in the sensitivity analysis (Table S3-2) was identical to the ranking of models in the main analysis (Table 3), with model S8 as the preferred model. Other models essentially had no support, as the second-best model S9 with one additional parameter provided little additional explanatory power (difference in deviance scores of 0.1, Table S3-2). Estimated coefficients under the AICc-preferred model S8 suggest overall survival differences among species, among rearing histories, and among years (Table S3-3). All else equal, survival probabilities were greater for sockeye than for coho and steelhead; greater for wild-reared than for hatchery-reared and rearing-unknown; and greater for 2005 than for 2007 (differences are calculated by re-defining the reference groups from Table S3-3 to be the groups with the highest estimated coefficients).

Incorporation of these fixed-effect intercepts did not qualitatively affect the estimates of fixed effect slopes with survival: significant positive slopes were still observed for body length and migration date in the Fraser River, a significant negative slope was still observed for illuminance in smaller rivers, and non-significant slopes from the main analysis (Table 4) remained non-significant in the sensitivity analysis (Table S3-3). Predicted effects of body length, sunlight intensity, and migration date on survival are shown in Figure S3-1 (section [i] of parts A–L) under this sensitivity model formulation, which mirror Figure 5.
from the main text. Random effect conditional modes for watersheds are shown in Figure S3-2. Relationships between migration date in lower river reaches and sunlight intensity associated with migration date are shown for separate species, rearing histories, and years in Figure S3-3, mirroring Figure 4 from the main text.

A second part of this sensitivity analysis involves allowing for additional interaction effects of species, rearing history, or year on survival. Building on model S9 (Table S3-2), the three interaction terms (between river size & body length; river size & light intensity; river size & migration date) were expanded to also be specific to different species, rearing history or year. This allows, for example, for the slopes between sunlight intensity and survival (which are already permitted to differ between the Fraser River and smaller rivers) to also differ among species. In abbreviated notation these additional sensitivity models are:

(S3-3a) \[ s \sim 1 + \text{Spp} + \text{HW} + \text{Year} + \text{TagType} + \text{FL} + \text{Rsize} + \text{Date} + \text{Light} + \ldots \text{Spp:Rsize:Date} + \text{Spp:Rsize:Light} + \text{Spp:Rsize:FL} | \text{rand}(\omega_{0*}) \]

(S3-3b) \[ s \sim 1 + \text{Spp} + \text{HW} + \text{Year} + \text{TagType} + \text{FL} + \text{Rsize} + \text{Date} + \text{Light} + \ldots \text{HW:Rsize:Date} + \text{HW:Rsize:Light} + \text{HW:Rsize:FL} | \text{rand}(\omega_{0*}) \]

(S3-3c) \[ s \sim 1 + \text{Spp} + \text{HW} + \text{Year} + \text{TagType} + \text{FL} + \text{Rsize} + \text{Date} + \text{Light} + \ldots \text{Year:Rsize:Date} + \text{Year:Rsize:Light} + \text{Year:Rsize:FL} | \text{rand}(\omega_{0*}) \]

Predicted survival relationships for these additional models are shown in sections [ii] of Figure S3-1. The formulations for slopes that differ by species (Eq. S3-3a), by rearing history (Eq. S3-3b), or by year (Eq. S3-3c) are shown in parts A–D, parts E–G, and parts H–L of Figure S3-1, respectively.
There are three reasons why the results from the main analysis are preferable to the results from this sensitivity analysis. First, the study design was not balanced with respect to combinations of species, rearing history, and year (Table 1). For example, there were no wild-reared sockeye groups, no Chinook in 2007, no wild-reared groups in 2007, and no Chinook, coho, or sockeye tagged and released in 2008 (Table 1). The lack of a fully-crossed design with respect to these variables means there may be confounding among these additive fixed effects in their effect on survival. Treating these instead as part of a “release group” random effect (along with watershed) alleviates the requirement for a balanced design.

Second, models from the main analysis (Table 3) outperformed models from the sensitivity analysis (Table S3-2) in terms of AICc scores. Comparing the preferred models from each set of candidate models, model S8 fit the data slightly better than model 8 (deviances of 2244.8 and 2247.6, respectively), but model S8 required estimating 18 parameters compared to only 9 parameters for model 8, such that the AICc score was much lower for model 8 (Table 3) than for model S8 (Table S3-2), giving a ΔAICc of 15.2 and suggesting essentially no support for the model with species, rearing history, and year treated as fixed effects.

Third, the treatment of species, rearing history, and year as fixed effects in an unbalanced design leave survival predictions susceptible to over-fitting. This is especially the case for the models in which effects of body length, illuminance, and migration date on survival are also allowed to vary by species, rearing history, or years (Eq. S3-3; sections [ii] of Figure S3-1), but also occurs for models that allow for only additive effects of species, rearing history, or years (Table S3-2; sections [i] of Figure S3-1). For example, it is
biologically unlikely that effects of migration date in the lower Fraser River on survival to coastal stations were actually negative in even years (Figures S3-1-H-i-e and S3-1-J-i-e) and positive in odd years (Figures S3-1-I-i-e and S3-1-K-i-e); this is more likely an artifact of different combinations of species and rearing histories being released in these years (Table 1). Similarly, despite the overall effect of lower survival for hatchery-reared fish compared with wild-reared fish (Table S3-3), predicted survival was greater for hatchery-reared fish in the Fraser River (Figure S3-1-E-i-c) compared to wild-reared fish in the Fraser River (Figure S3-1-F-i-c) as a result of confounding with other variables. Overfitting is also apparent in the relationships between migration date in lower river reaches and associated sunlight levels (Figure S3-3). Loess smoother fits to the data subsets of single species, rearing histories, or years were often erratic, particularly for categories with small sample sizes, whereas the pattern across the full dataset seemed to provide a better comparison between the Fraser River and smaller rivers (Figure 4).
Table S3-1. Predictor variables contained in logistic regression models for sensitivity analysis with species, rearing history, and year as fixed effects. Response variable is the joint probability of survival from lower river reaches to coastal detection stations and detection at those coastal stations.

<table>
<thead>
<tr>
<th>Predictor variable</th>
<th>Model</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>S1</td>
</tr>
<tr>
<td>Fixed effects</td>
<td></td>
</tr>
<tr>
<td>Species (“Spp”)</td>
<td>x</td>
</tr>
<tr>
<td>Rearing history (“HW”)</td>
<td>x</td>
</tr>
<tr>
<td>Year</td>
<td>x</td>
</tr>
<tr>
<td>Tag model (“TagType”)</td>
<td>x</td>
</tr>
<tr>
<td>Body length (“FL”)</td>
<td>x</td>
</tr>
<tr>
<td>Fraser River / non-Fraser (“Rsize”)</td>
<td>x</td>
</tr>
<tr>
<td>Date of lower river detection (“Date”)</td>
<td>x</td>
</tr>
<tr>
<td>Illuminance during lower river detection (“Light”)</td>
<td>x</td>
</tr>
<tr>
<td>Rsize:Date interaction</td>
<td>x</td>
</tr>
<tr>
<td>Rsize:Light interaction</td>
<td>x</td>
</tr>
<tr>
<td>Rsize:FL interaction</td>
<td>x</td>
</tr>
<tr>
<td>Random effect</td>
<td></td>
</tr>
<tr>
<td>Watershed ((ω_{0,i}))</td>
<td>x</td>
</tr>
</tbody>
</table>
Table S3-2. Comparison of mixed-effects logistic regression models for sensitivity analysis with species, rearing history, and year as fixed effects.

<table>
<thead>
<tr>
<th>Model</th>
<th>–2·\ln(L)</th>
<th>df</th>
<th>AICc</th>
<th>ΔAICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>S8.</td>
<td>2244.8</td>
<td>18</td>
<td>2280.8</td>
<td>0.0</td>
</tr>
<tr>
<td>S9.</td>
<td>2244.7</td>
<td>19</td>
<td>2282.7</td>
<td>1.9</td>
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<tr>
<td>S6.</td>
<td>2257.4</td>
<td>17</td>
<td>2291.4</td>
<td>10.6</td>
</tr>
<tr>
<td>S7.</td>
<td>2258.1</td>
<td>17</td>
<td>2292.1</td>
<td>11.3</td>
</tr>
<tr>
<td>S5.</td>
<td>2269.9</td>
<td>16</td>
<td>2301.9</td>
<td>21.1</td>
</tr>
<tr>
<td>S4.</td>
<td>2287.0</td>
<td>14</td>
<td>2315.0</td>
<td>34.2</td>
</tr>
<tr>
<td>S3.</td>
<td>2294.2</td>
<td>14</td>
<td>2322.2</td>
<td>41.4</td>
</tr>
<tr>
<td>S2.</td>
<td>2306.7</td>
<td>14</td>
<td>2334.7</td>
<td>53.9</td>
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<tr>
<td>S1.</td>
<td>2310.3</td>
<td>13</td>
<td>2336.3</td>
<td>55.5</td>
</tr>
</tbody>
</table>

Criteria include the deviance (twice the negative log-likelihood, –2·\ln(L)), degrees of freedom (df), Akaike Information Criterion adjusted for sample size (AICc), and difference in AICc from the AICc-best model.

\(^a\) base model is: \(s \sim 1 + \text{Spp} + \text{HW} + \text{Year} + \text{TagType} + \text{FL} \mid \text{rand}(\omega_0, \omega_1)\), where \(s\) is a joint probability of survival and detection.
Table S3-3. Estimated coefficients of fixed effects for model S8, the AICc-preferred model in sensitivity analysis with species, rearing history, and year as fixed effects.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>lower 95% CL</th>
<th>upper 95% CL</th>
<th>z^a</th>
</tr>
</thead>
<tbody>
<tr>
<td>Overall intercept</td>
<td>−0.986</td>
<td>−2.129</td>
<td>0.157</td>
<td>−1.69</td>
</tr>
<tr>
<td>Spp/coho</td>
<td>−1.121</td>
<td>−2.285</td>
<td>0.044</td>
<td>−1.89</td>
</tr>
<tr>
<td>Spp/sockeye</td>
<td>1.513</td>
<td>−0.477</td>
<td>3.502</td>
<td>1.49</td>
</tr>
<tr>
<td>Spp/steelhead</td>
<td>−0.798</td>
<td>−1.940</td>
<td>0.343</td>
<td>−1.37</td>
</tr>
<tr>
<td>HW/unknown</td>
<td>−0.690</td>
<td>−2.047</td>
<td>0.667</td>
<td>−1.00</td>
</tr>
<tr>
<td>HW/wild</td>
<td>0.607</td>
<td>0.225</td>
<td>0.988</td>
<td>3.12</td>
</tr>
<tr>
<td>Year/2005</td>
<td>0.273</td>
<td>−0.079</td>
<td>0.626</td>
<td>1.52</td>
</tr>
<tr>
<td>Year/2006</td>
<td>0.034</td>
<td>−0.305</td>
<td>0.372</td>
<td>0.19</td>
</tr>
<tr>
<td>Year/2007</td>
<td>−0.215</td>
<td>−0.600</td>
<td>0.169</td>
<td>−1.10</td>
</tr>
<tr>
<td>Year/2008</td>
<td>0.054</td>
<td>−0.667</td>
<td>0.775</td>
<td>0.15</td>
</tr>
<tr>
<td>TagType/V9</td>
<td>0.045</td>
<td>−0.434</td>
<td>0.523</td>
<td>0.18</td>
</tr>
<tr>
<td>FL</td>
<td>0.458</td>
<td>0.258</td>
<td>0.658</td>
<td>4.49</td>
</tr>
<tr>
<td>Rsize/non-Fraser</td>
<td>1.374</td>
<td>0.144</td>
<td>2.604</td>
<td>2.19</td>
</tr>
<tr>
<td>Rsize/Fraser:Light</td>
<td>0.006</td>
<td>−0.179</td>
<td>0.191</td>
<td>0.06</td>
</tr>
<tr>
<td>Rsize/non-Fraser:Light</td>
<td>−0.452</td>
<td>−0.615</td>
<td>−0.290</td>
<td>−5.45</td>
</tr>
<tr>
<td>Rsize/Fraser:Date</td>
<td>0.587</td>
<td>0.362</td>
<td>0.811</td>
<td>5.13</td>
</tr>
<tr>
<td>Rsize/non-Fraser:Date</td>
<td>0.026</td>
<td>−0.212</td>
<td>0.265</td>
<td>0.22</td>
</tr>
</tbody>
</table>

Numerical covariates were centered and standardized by their standard deviations.
To ease comparisons, the model is specified with slopes for “Date” and “Light” that are specific to Fraser and non-Fraser rivers rather than specified with main effects and interaction discrepancies as shown in Table S3-2, but these two models are statistically identical.

\[ |z| > 2 \] generally suggests statistical significance at \( \alpha = 0.05 \).

Reference groups:

- \(^{b}\) “Chinook”
- \(^{c}\) “hatchery”
- \(^{d}\) “2004”
- \(^{e}\) “V7”
- \(^{f}\) “Fraser”
Figure S3-1 (on following pages). Sensitivity analyses for the predicted joint probability of survival from lower river reaches to coastal detection stations and detection at those stations for the Fraser River and smaller rivers as a function of: body length, average light intensity during crossing events, and the Julian day of first detection. Sensitivity analyses treat species, rearing history, and year as fixed effects instead of as a part of release group random effects. For each of parts (A–L), section [i] shows predictions with only additive fixed effects of species, rearing history, and year (thus resulting in separate intercepts in logit-space), while section [ii] shows predictions under a model in which interactions are also permitted with fork length, illuminance, and migration date (thus resulting in separate slopes for each of these variables and for each river size as well as separate intercepts in logit-space). Interactions with these variables occur for species (A–D), rearing histories (E–G), or years (H–L). Within each section, the layout of panels a-f and formatting mirror those of Figure 5. Data points show survival predictions of individual fish from fixed-effects logistic regression versions of: [i] model S8 (Table S3-3), or [ii] with additional interactions allowed (Eq. S3-3), restricted to the subset of a particular species, rearing history, or year. Fitted lines show the mean predicted survival with dashed 95% confidence bands, also restricted to the subset of a particular species, rearing history, or year.
Figure S3-1-A. Sensitivity analyses with species fixed effects that are [i] additive, or [ii] interact with fork length, illuminance, and migration date. Results shown for Chinook.
[i] Species – coho, additive model

![Graphs showing predicted survival to ocean vs. fork length, illuminance, and Julian day in lower river for Fraser River and smaller rivers.]

[ii] Species – coho, interaction model

![Graphs showing predicted survival to ocean vs. fork length, illuminance, and Julian day in lower river for Fraser River and smaller rivers.]

Figure S3-1-B. Sensitivity analyses with species fixed effects that are [i] additive, or [ii] interact with fork length, illuminance, and migration date. Results shown for coho.
[i] Species – sockeye, additive model

![Graphs showing predicted survival to ocean with additive model for Fraser River and smaller rivers.](image)

[ii] Species – sockeye, interaction model

![Graphs showing predicted survival to ocean with interaction model for Fraser River and smaller rivers.](image)

Figure S3-1-C. Sensitivity analyses with species fixed effects that are [i] additive, or [ii] interact with fork length, illuminance, and migration date. Results shown for sockeye.
[i] Species – steelhead, additive model

Figure S3-1-D. Sensitivity analyses with species fixed effects that are [i] additive, or [ii] interact with fork length, illuminance, and migration date. Results shown for steelhead.
[i] Rearing history – hatchery, additive model

Figure S3-1-E. Sensitivity analyses with rearing history fixed effects that are [i] additive, or [ii] interact with fork length, illuminance, and migration date. Results shown for hatchery-reared.
[i] Rearing history – wild, additive model

Figure S3-1-F. Sensitivity analyses with rearing history fixed effects that are [i] additive, or [ii] interact with fork length, illuminance, and migration date. Results shown for wild-reared.
[i] Rearing history – unknown, additive model

![Graphs showing predicted survival to ocean for Fraser River and smaller rivers.](image)

[ii] Rearing history – unknown, additive model

![Graphs showing predicted survival to ocean for Fraser River and smaller rivers.](image)

Figure S3-1-G. Sensitivity analyses with rearing history fixed effects that are [i] additive, or [ii] interact with fork length, illuminance, and migration date. Results shown for rearing-unknown.
[i] Year – 2004, additive model

![Graphs showing survival to ocean for Fraser River and smaller rivers with additive model.](image)

[ii] Year – 2004, interaction model

![Graphs showing survival to ocean for Fraser River and smaller rivers with interaction model.](image)

Figure S3-1-H. Sensitivity analyses with year fixed effects that are [i] additive, or [ii] interact with fork length, illuminance, and migration date. Results shown for 2004.
[i] Year – 2005, additive model

Figure S3-1-I. Sensitivity analyses with year fixed effects that are [i] additive, or [ii] interact with fork length, illuminance, and migration date. Results shown for 2005.
[i] Year – 2006, additive model

Figure S3-1-J. Sensitivity analyses with year fixed effects that are [i] additive, or [ii] interact with fork length, illuminance, and migration date. Results shown for 2006.
[i] Year – 2007, additive model

![Graphs showing predicted survival to ocean](image)

[ii] Year – 2007, interaction model

![Graphs showing predicted survival to ocean](image)

Figure S3-1-K. Sensitivity analyses with year fixed effects that are [i] additive, or [ii] interact with fork length, illuminance, and migration date. Results shown for 2007.
[i] Year – 2008, additive model

Figure S3-1-L. Sensitivity analyses with year fixed effects that are [i] additive, or [ii] interact with fork length, illuminance, and migration date. Results shown for 2008.

[ii] Year – 2008, interaction model
Figure S3-2. Sensitivity analysis for random effect conditional modes of watershed for mixed-effects logistic regression. Sensitivity analyses treat species, rearing history, and year as fixed effects instead of as part of release group random effects. The response is the joint probability of survival from lower river to coastal waters and detection at coastal stations. Conditional modes are survival offsets from the overall fixed-effect intercept in logit space. Conditional modes estimated under model S8 are shown separately for Fraser River tributaries (top block) and smaller rivers (bottom block). Error bars show standard deviations around conditional modes.
Figure S3-3 (on following pages). Sensitivity analyses for the relationship between Julian day of first detection in lower river reaches and corresponding light intensity during crossing events. Sensitivity analyses subset the data by separate: (A) species; (B) rearing histories; or (C) years. Within each section [x] of parts (A–C), the layout of panels a-b and formatting mirror those of Figure 4. Data points show individual salmon smolts from (a) the Fraser River, and (b) smaller rivers. Locally-weighted polynomial regression predicted means and 95% confidence bands are plotted (loess fits, with smoothing parameter values of 2/3) for (a) and (b) separately.
[i] Species – Chinook

![Graph](image1)

Julian day first detected in lower river

[ii] Species – coho

![Graph](image2)

Julian day first detected in lower river

[iii] Species – sockeye

![Graph](image3)

Julian day first detected in lower river

[iv] Species – steelhead

![Graph](image4)

Julian day first detected in lower river

Figure S3-3-A. Sensitivity analyses for separate species.
Figure S3-3-B. Sensitivity analyses for separate rearing histories.
Figure S3-3-C (continued next page). Sensitivity analyses for separate years.
[v] Year – 2008

Figure S3-3-C (cont.). Sensitivity analyses for separate years.
Supplementary material 4. Sensitivity analysis for effects of illuminance on survival

Light intensity may influence survival in various ways. In the key run, described in the main text, illuminance at the time of the first detection of each crossing event was calculated, and was then averaged over all crossing events in lower river reaches. (A crossing event consists of the sequence of detections of an individual fish at an individual receiver station, in which no more than 60 minutes may elapse between successive detections.) In this sensitivity run, rather than averaging illuminance values, the maximum illuminance at the time of first detection of each crossing event was taken out of all possible crossing events in lower river reaches. Biologically, what might affect the chance of survival most is not average exposure to visual predation risk, but maximum exposure.

The mixed-effects logistic regression analysis was repeated by considering the maximum illuminance instead of average illuminance in lower river reaches. Table S4-1 shows model comparison results for the sensitivity run, paralleling those from Table 2 of the main text for the key run. Results are similar to those of the key run, with model 8 again as the AICc-preferred model. Table S4-2 shows estimated coefficients of fixed effects for the sensitivity run, paralleling those from Table 3 of the main text for the key run. Results are similar to those of the key run.

The sensitivity analysis is extended to visual comparisons. In considering the maximum light intensity rather than the average light intensity across lower river crossing events, illuminance values increased for Fraser River fish (Figure S4-1a) compared to the key run in the main text (Figure 4a) early in the migration season, when most salmon smolts were exposed to high maximum light intensity. Later in the migration season, there was little difference in illuminance values based on the maximum (Figure S4-1a) or on calculated averages (Figure 4a).
For salmon smolts in smaller rivers, there was little difference between illuminance levels based on the maximum (Figure S4-1a) or on averages (Figure 4a) throughout the migration season. This was expected given that smolts avoided travel in lower river reaches during daylight hours, i.e., the maximum light intensity at night is not much greater than the average light intensity at night, both are low. There was little difference between the key run (Figure 5c,d) and the sensitivity run (Figure S4-2c,d) in the effects of light intensity on survival, for smolts from either the Fraser River or smaller rivers. This suggests that there was little difference between the effects of average exposure and maximum exposure to visual predation risk in lower river reaches on survival through the estuary to marine waters. Finally, Figure S4-3 shows conditional modes of the release group random intercepts under the sensitivity run, paralleling those from Figure S3-1 for the key run. Results are similar to the key run, with minor changes in the modes of some release groups.

Overall, analyses appear to be robust to assumptions of different metrics for quantifying light intensity.
Table S4-1. Comparison of candidate models for the joint probability of survival to coastal detection stations and detection at those coastal stations, for the sensitivity analysis of maximum illuminance in lower river

<table>
<thead>
<tr>
<th>Model</th>
<th>(-2 \cdot \ln(L))</th>
<th>(df)</th>
<th>AICc</th>
<th>ΔAICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>8.  (\ldots + \text{Rsize} + \text{Date} + \text{Light} + \text{Rsize:Date} + \text{Rsize:Light})</td>
<td>2296.6</td>
<td>9</td>
<td>2314.6</td>
<td>0.0</td>
</tr>
<tr>
<td>9.  (\ldots + \text{Rsize} + \text{Date} + \text{Light} + \text{Rsize:Date} + \text{Rsize:Light} + \text{Rsize:FL})</td>
<td>2295.7</td>
<td>10</td>
<td>2315.7</td>
<td>1.1</td>
</tr>
<tr>
<td>6.  (\ldots + \text{Rsize} + \text{Date} + \text{Light} + \text{Rsize:Light})</td>
<td>2307.5</td>
<td>8</td>
<td>2323.5</td>
<td>8.9</td>
</tr>
<tr>
<td>7.  (\ldots + \text{Rsize} + \text{Date} + \text{Light} + \text{Rsize:Date})</td>
<td>2316.1</td>
<td>8</td>
<td>2332.1</td>
<td>17.5</td>
</tr>
<tr>
<td>5.  (\ldots + \text{Rsize} + \text{Date} + \text{Light})</td>
<td>2325.2</td>
<td>7</td>
<td>2339.2</td>
<td>24.6</td>
</tr>
<tr>
<td>4.  (\ldots + \text{Light})</td>
<td>2331.4</td>
<td>5</td>
<td>2341.4</td>
<td>26.8</td>
</tr>
<tr>
<td>3.  (\ldots + \text{Date})</td>
<td>2343.9</td>
<td>5</td>
<td>2353.9</td>
<td>39.3</td>
</tr>
<tr>
<td>2.  (\ldots + \text{Rsize})</td>
<td>2347.1</td>
<td>5</td>
<td>2357.1</td>
<td>42.5</td>
</tr>
<tr>
<td>1.  base model</td>
<td>2350.6</td>
<td>4</td>
<td>2358.6</td>
<td>44.0</td>
</tr>
</tbody>
</table>

See Table 2 caption for further details
Table S4-2. Estimated coefficients of fixed effects for model 8, for the sensitivity analysis of maximum illuminance in lower river reaches

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate</th>
<th>lower 95% CL</th>
<th>upper 95% CL</th>
<th>z</th>
</tr>
</thead>
<tbody>
<tr>
<td>Overall intercept</td>
<td>-0.900</td>
<td>-1.656</td>
<td>-0.145</td>
<td>-2.34</td>
</tr>
<tr>
<td>TagType/V9</td>
<td>0.231</td>
<td>-0.381</td>
<td>0.843</td>
<td>0.74</td>
</tr>
<tr>
<td>FL</td>
<td>0.465</td>
<td>0.265</td>
<td>0.664</td>
<td>4.56</td>
</tr>
<tr>
<td>Rsize/non-Fraser</td>
<td>0.599</td>
<td>-0.200</td>
<td>1.398</td>
<td>1.47</td>
</tr>
<tr>
<td>Rsize/Fraser:Light</td>
<td>0.022</td>
<td>-0.148</td>
<td>0.191</td>
<td>0.25</td>
</tr>
<tr>
<td>Rsize/non-Fraser:Light</td>
<td>-0.546</td>
<td>-0.736</td>
<td>-0.356</td>
<td>-5.64</td>
</tr>
<tr>
<td>Rsize/Fraser:Date</td>
<td>0.666</td>
<td>0.332</td>
<td>1.000</td>
<td>3.91</td>
</tr>
<tr>
<td>Rsize/non-Fraser:Date</td>
<td>-0.142</td>
<td>-0.485</td>
<td>0.201</td>
<td>-0.81</td>
</tr>
</tbody>
</table>

See Table 3 caption for further details
Figure S4-1. Sensitivity analysis of illuminance at the time of detection plotted against Julian day of first detection in lower river reaches. In the key run, average illuminance during crossing events was calculated over all lower river crossing events of an individual fish (Figure 4 of main text). In this sensitivity run, the maximum illuminance during crossing events was taken from all lower river crossing events of an individual fish. See Figure 4 caption for further details.
Figure S4-2. Sensitivity analysis for effects of light intensity at the time of lower river detection on the joint probability of survival to coastal detection stations and detection at those stations. In the key run, average illuminance during crossing events was calculated over all lower river crossing events (Figure 5 of main text). In this sensitivity run, the maximum illuminance at the time of first detection of a crossing event was taken from all lower river crossing events. See Figure 5 caption for further details.
Figure S4-3. Conditional modes of release groups for the sensitivity analysis of maximum illuminance in lower river reaches (rather than average illuminance for the key run, as shown in Figure 6 of main text). See Figure 6 caption for further details.